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A PALEOCENE OSTRACODE FAUNA FROM THE COAL BLUFF MARL MEMBER OF THE NAHEOLA FORMATION OF ALABAMA[1]

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ABSTRACT—Thirty-eight species of ostracodes, nineteen new, and one new genus are described from material collected from the Coal Bluff marl member of the Naheola formation (U. Midway) near Caledonia, Wilcox County, Alabama. Where enough specimens are present, a description is given of molts and sexual dimorphism.

INTRODUCTION

THE ostracode fauna described in this report was obtained from the Coal Bluff marl member of the Naheola formation from the creek bed near the town of Caledonia, Wilcox County, Alabama, in the SW¼ Sec. 29, T 11 N, R 10 E. In 1944 Cushman described a rich foraminiferal fauna from the same locality.

The author wishes to thank Dr. Lyman D. Toulmin, of Florida State University, Mrs. Betty Kellett Nadeau, formerly of Washington University, for valuable guidance and criticism, and Dr. H. V. Howe for access to the ostracode collection of Louisiana State University. Thanks are extended to Mr. John Etter, now with Sinclair Oil and Refining Company, Tulsa, Oklahoma, for his valuable guidance in photographing the specimens.

[1] Based on a thesis submitted to the Graduate Board of Washington University, St. Louis, Mo., in partial fulfillment of the Master of Arts degree.

Before being photographed some of the specimens were darkened by the silver nitrate process first introduced by Triebel (1947, pp. 29–39), translated by Levinson (1951, p. 27), and further developed by Mr. John Etter.

The type specimens have been deposited in the American Museum of Natural History.

SYSTEMATIC DESCRIPTIONS

Order OSTRACODA Latreille, 1801
Suborder PLATYCOPA SARS, 1865 (1866)
Family CYTHERELLIDAE SARS, 1865 (1866)
Genus CYTHERELLA Jones, 1849

Cytherella JONES, 1849, Mon. Entom. Cret. England, Palaeont. Soc. London, p. 28.

Type species: *Cytherina ovata* Roemer, 1840, Verstein. Norddeutsch. Kreid., p. 104, pl. 16, fig. 21. Subs. design. Ulrich, 1894, Geol. Minnesota, p. 684.

CYTHERELLA TUMIDOSA Alexander, 1934
Plate 1, figures 3, 11, 16, 17

Cytherella tumidosa ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 209–210, pl. 32, figs. 1, 2, 5, 6; pl. 35, figs. 3, 4.
Cytherella tumidosa HARRIS & JOBE, 1951, Microfauna Midway Ark., pp. 67, 68, pl. 11, fig. 3.

Remarks.—The young represent almost half of the specimens present and can be separated easily into sexes due to the fact that the young female carapace is shorter and higher than the young male and exhibits a strongly tumid postventral area. The youngest double valve shows a narrow overlap on the dorsal and ventral margins, but a very indistinct overlap on the ends. Some of the smallest valves are transparent. Both sexes of the young show a greater tumidity in the postventral portion of the carapace. Fewer males than females, both young and adult, were present in this Midway fauna.

Dimensions of figured specimens.—Female, right valve, length .91 mm., height .65 mm., left valve, length .82 mm., height .53 mm. Male, right valve, length .84 mm., height .53 mm., left valve, length .82 mm., height .47 mm.

Hypotype.—AMNH (double valve) OT-100.

Occurrence.—This is the most common genus and species in the Coal Bluff material. Alexander reports it as common in the Wills Point formation and rare in the Kincaid formation of Texas. Toulmin (1940, range chart), (1951, p. 56) lists it as rare in the Salt Mountain and Nanafalia formations of Alabama. Harris and Jobe report it as common in the Midway of Arkansas.

Genus MORROWINA Loetterle, 1937

Morrowina LOETTERLE, 1937, Nebraska Geol. Surv., Bull. 12, p. 51.

Type species: *Cytherella excavata* Alexander, 1934, Jour. Paleontology, vol. 8, pp. 211–212, pl. 32, figs. 3, 4; pl. 35, figs. 5, 6.

MORROWINA EXCAVATA (ALEXANDER), 1934
Plate 1, figures 1, 2, 9, 10

Cytherella beyrichi JONES, 1856 (non. *C. beyrichi* Reuss, 1851), Mon. Tert. Entom. England, Palaeont. Soc. London, p. 55, pl. 5, fig. 12.
Cytherella excavata ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 211–212, pl. 32, figs. 3, 4; pl. 35, figs. 5, 6.

Remarks.—The shallow, subcircular pit sets off this genus from *Cytherella*. The muscle scar pattern in this species coincides with the pit. The pit and scar are well to the posterior in the young, but are nearer to the anterior as the carapace increases in size, due to the greater development of the posterior during growth. The overlap in the young is very narrow with the greatest posterior tumidity shown by the smallest molts. As in *Cytherella*, there are approximately twice as many females as males present.

Dimensions of figured specimens.—Female, right valve, length .71 mm., height .44 mm., left valve, length .61 mm., height .46 mm. Male, right valve, length .56 mm., height .34 mm., left valve, length .61 mm., height .35 mm.

Hypotype.—AMNH (right valve) OT-101; (left valve) OT-102.

Occurrence.—Rather common in the Coal Bluff. Alexander found it to be rare at most localities of the Wills Point and Kincaid formations of Texas. Harris and Jobe report it as rather common in the Midway of Arkansas.

Genus CYTHERELLOIDEA Alexander, 1929

Cytherelloidea ALEXANDER, 1929, Univ. Texas Bull. 2907, p. 55.
Cytherelloidea HOWE, 1934, Jour. Paleontology, vol. 8, p. 27.
Cytherelloidea SEXTON, 1951, Jour. Paleontology, vol. 25, pp. 808–816.

Type species: *Cythere* (*Cytherella*) *williamsoniana* Jones, 1849, Mon. Entom. Cret. England, Palaeont. Soc. London, p. 31, pl. 7, figs. 26a–26i.

Description.—Carapace small, quadrangular to oblong-ovate. Usually thickest posteriorly. Right valve larger than the left. Overlap usually prominent only at dorsal and posterior margins. Surface ornamentation highly variable, consisting of ridges, pits, tubercles on the posterior end; when present, the ridges tend to be aligned with the long axis of the carapace and to become more complex as the genus rises in the geologic section.

Hinge simple, consisting of a groove in the right valve and a flange in the left. Muscle scar pattern consists of two narrow rows of approximately seven elements each. In most species the scar pattern coincides with the pit on the exterior. Van den Bold (1946) notes that the genus has the same pronounced sexual dimorphism as *Cytherella*,

the shell of the female being higher and broader than the male, especially at the posterior end. The females sometimes show two deep, internal, posterior pits. According to Kellett (personal communication) the genus may have stemmed from some such sulcate Paleozoic genus as *Sulcella* Coryell and Sample, 1932, or *Tetratylus* Cooper, 1941.

CYTHERELLOIDEA TOMBIGBEENSIS subsp. DELICATA Howe, 1934
Plate 1, figures 18–21

Cytherelloidea tombigbeensis var. *delicata* HOWE, 1934, Jour. Paleontology, vol. 8, p. 30.

Remarks.—Internally the females show two pits on the posterior portion of the carapace. The hingement is typical for the genus except that a few of the largest specimens show a widening of the hinge groove below the projection of the dorsal margin which forms the overlap; obscure crenulations, especially pronounced in the widened area, appear on the dorsal portion of the groove. The groove is partially terminated on the anterior by a very narrow, low, obscure transverse ridge.

With increase in size the posterior end of the carapace becomes more angular, although the angularity is not pronounced at any stage. With increase in size, the carapace also becomes more flattened, the ventral ridge of the youngest molt being relatively high and pronounced. In the smallest molts, the well-defined dorsal ridge does not always extend toward the posterior margin as in the adults, and the offshoot curves sharply downward inside the upswing of the prominent ventral ridge; this ridge bordering the posterior edge of the depression is very prominent in the young, but becomes obscure as the carapace increases in size. In female gerontic forms the posterior portion of the well-developed dorsal and ventral ridges merge to form a thick knob-like ridge; on the interior of the valves two cup-shaped depressions are found which coincide with the thickened portion on the exterior of the carapace. This structure was first illustrated by Van Veen (1932, plates 15–22).

Dimensions of figured specimens.—Female, right valve, gerontic form, length .59 mm., height .36 mm., left valve, length .53 mm., height .30 mm. Male, right valve, length .48 mm., height .29 mm., left valve, length .47 mm., height .26 mm.

Hypotypes.—AMNH (right valve) OT-103; (left valve) OT-104.

Occurrence.—Rather rare in the Coal Bluff. Originally described by Howe from the Matthews Landing marl member of the Porters Creek formation.

CYTHERELLOIDEA TRIEBELI Munsey, n. sp.
Plate 1, figure 6

Description.—Carapace small, elongate, somewhat compressed. Anterior half of the dorsal margin straight to slightly concave, gently tapering over posterior half; anterior broadly rounded; ventral margin gently concave; posterior margin somewhat truncated, less rounded than the anterior. Greatest thickness at the posterior. A small, deep, oblong pit or depression is located dorsal and posterior to the center. Circumscribing the entire periphery of the carapace is a low marginal ridge. A fairly well-defined knob lies near the postdorsal angle, and separated ventrally from it by a shallow groove is another low knob which extends anteriorly as a low ventral ridge dying out in the anterior half of the valve. Bordering the anterodorsal edge of the pit is a low ridge, intersecting and not quite perpendicular to the marginal ridge; anterior to this ridge and separated by a shallow depression is a similar short ridge. Surface covered by rather well-defined, shallow reticulations. Hingement and muscle scar pattern typical of the genus.

Dimensions of figured specimen.—Length .38 mm., height .24 mm.

Holotype.—AMNH (left valve) OT-105.

Occurrence.—Very rare in the Coal Bluff at Caledonia.

Remarks.—Only two well-preserved specimens of this species were found, both left valves. Both specimens were small and it may be that they were not fully mature forms. This species is very similar to *C. irregularis* (Brady) but is distinguished by its flattened anterior depression. The species is named in honor of Dr. E. Triebel, Natur-Museum Senckenberg, Frankfurt am Main, American Zone, Germany.

CYTHERELLOIDEA ERRONECOSTATA Munsey, n. sp.
Plate 1, figures 12, 13

Description.—Carapace small, subquadrate. Dorsal margin gently arched; anterior broadly rounded; ventral margin somewhat

strongly concave in middle; posterior obliquely truncated. A broad, shallow pit or depression is situated slightly dorsal to the center of the carapace and corresponds in position to the muscle scar on the inner surface. A well-defined ridge begins at the postdorsal angle, extends along the dorsum and around the anterior just short of the edge, forms a marginal rim along the venter, and becomes well elevated on the posterior end of the valve. At the postdorsal angle it curves inward and dies out in the anterior portion of the carapace. Beneath this ridge and separated from it by a shallow groove is another prominent ridge which originates in the anterior portion of the central depression and extends anteriorly almost to the anterior marginal ridge. A shallow groove separates this ventrally from another prominent ridge which extends posteriorly beneath the depression, curves upward and backward to join with the main dorsal ridge at the postdorsal edge of the pit. Ventral to this ridge another ridge begins just short of the posterior rim, curves gently downward and extends anteriorly, dying out just before reaching the anteroventral rim. Surface covered by evenly distributed, well-defined reticulations. Hingement, muscle scar typical of genus, dimorphism obscure. The young show a proportionally more inflated posterior as well as more truncation in the postventral portion of the carapace.

Dimensions of figured specimens.—Right valve, length .44 mm., height .27 mm., left valve, length .42 mm., height .25 mm.

Holotype.—AMNH (right valve) OT-106; paratype (left valve) OT-107.

Occurrence.—Rather common.

Remarks.—This species differs from *C. spiralia* Jennings (1) in not having the central depression extending posteriorly to the groove within the marginal rim, (2) in the more truncated and elevated posterior, and (3) in having a definite ridge beginning in the anterior portion of the depression and extending between the prominent dorsal and middle ridges.

CYTHERELLOIDEA NANOPLEURA
Munsey, n. sp.
Plate 1, figure 5

Description.—Right valve small, oblong-ovate, highest at the middle. Dorsal margin strongly arched; anterior end broadly rounded; ventral margin rather strongly convex; posterior somewhat obliquely rounded. Thickest at the posterior. A distinct oval depression is situated slightly dorsal to the center of the carapace. A marginal rim is formed on all edges by a low ridge. Another low, very indistinct ridge begins at the anteroventral angle, extends posteriorly parallel to the ventral marginal ridge and curves upward for a short distance parallel to and dying out just short of the postventral angle. The smaller left valve is more quadrate than the right and is less curved at the dorsal and ventral margins; the dorsal margin is nearly straight for most of its length, but tapers rather sharply at the postdorsal angle. Small, distinct pits are evenly distributed over the surface. Internal features typical of the genus.

Dimensions of the figured specimen.—Length .56 mm., height .32 mm.

Holotype.—AMNH (left valve) OT-108; paratype (right valve) OT-109.

EXPLANATION OF PLATE 1

FIGS. *1, 2, 9, 10—Morrowina excavata* (Alexander). *1*, female, left valve, ×60. *2*, male, left valve, ×60. *9*, female, right valve, ×45. *10*, male, right valve, ×68. (p. 2)

3, 11, 16, 17—Cytherella tumidosa Alexander. *3*, male, left valve, ×45. *11*, male, right valve, ×50. *16*, female, right valve, ×40. *17*, female, left valve, ×40. (p. 2)

4—Platella kellettae Munsey, n. sp. Left valve, ×58. (p. 5)

5—Cytherelloidea nanopleura Munsey, n. sp. Right valve, ×50. (p. 4)

6—Cytherelloidea triebeli Munsey, n. sp. Left valve, ×60. (p. 3)

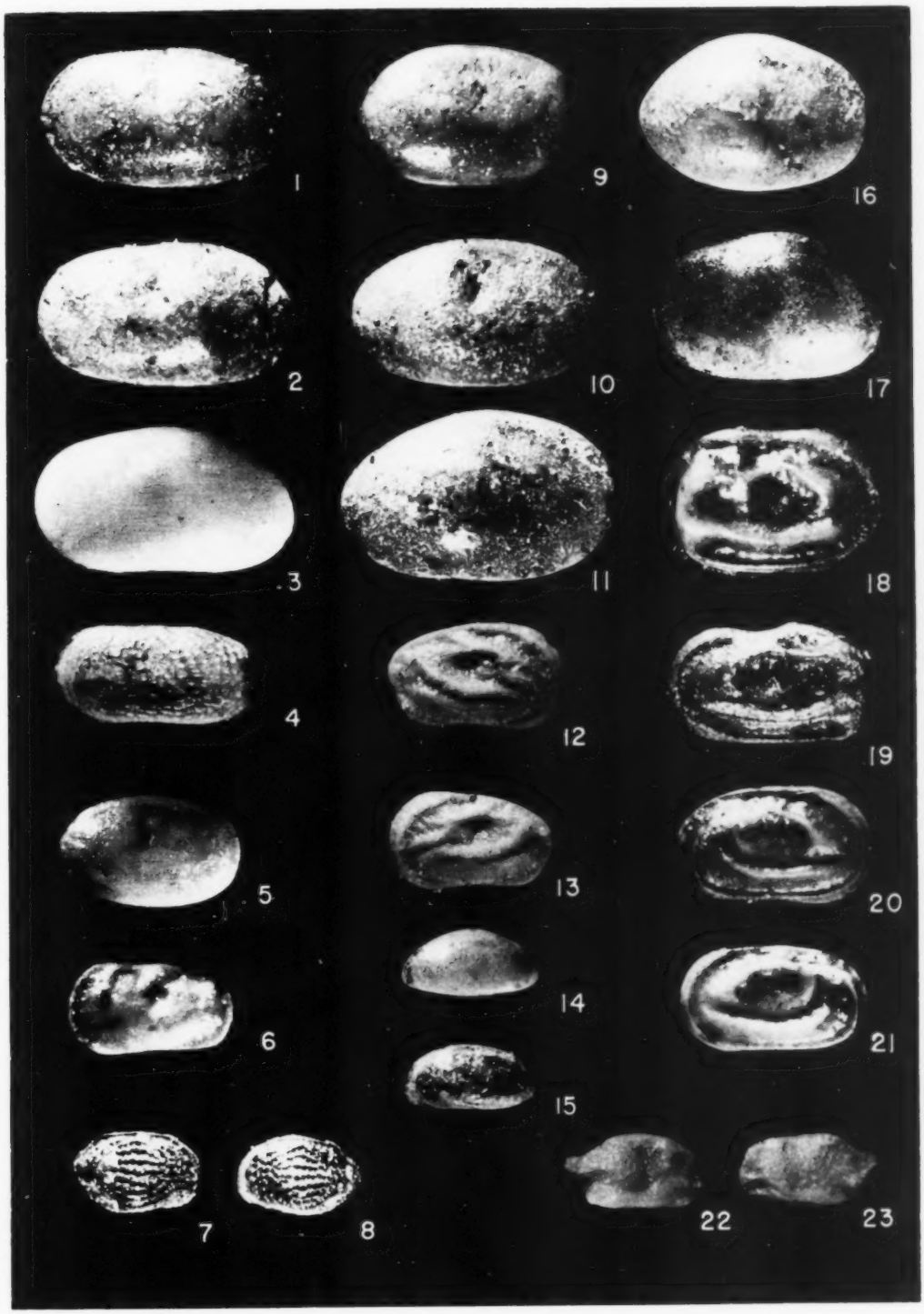
7, 8—Loxoconcha corrugata Alexander. *7*, right valve, ×60. *8*, left valve, ×60. (p. 16)

12, 13—Cytherelloidea erronecostata Munsey, n. sp. *12*, right valve, ×60. *13*, left valve, ×57. (p. 3)

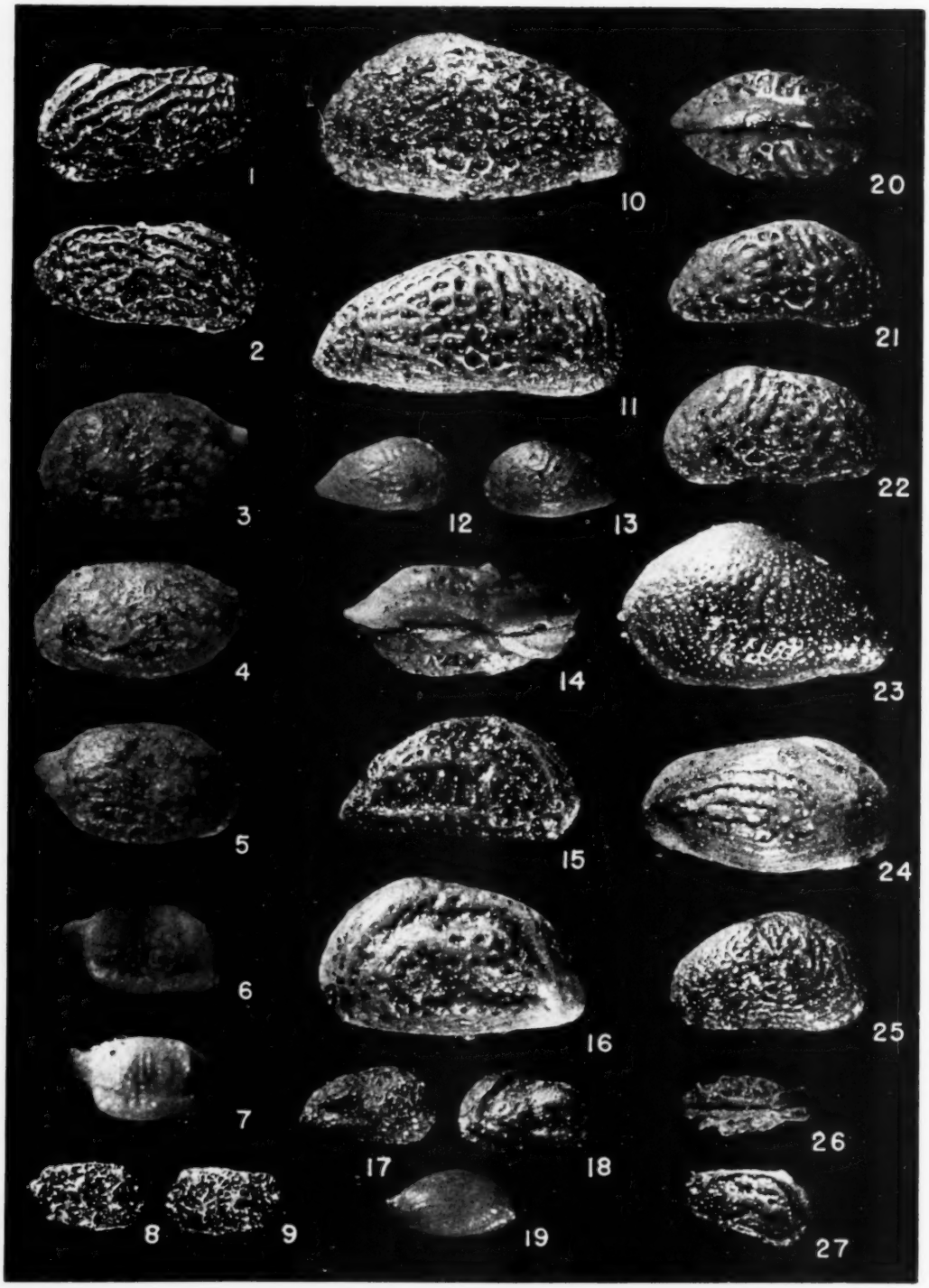
14, 15—Microxestoleberis westmorelandi Munsey, n. sp. *14*, right valve, ×52. *15*, left valve, ×60. (p. 19)

18–21—Cytherelloidea tombigbeensis subsp. *delicata* Howe. *18*, female, gerontic form, right valve, ×58. *19*, female, late adult, left valve, ×58. *20*, male, right valve, ×62. *21*, male, left valve, ×60. (p. 3)

22–23—Cytherura oxycruris Munsey, n. sp. *22*, right valve, ×58. *23*, left valve, ×55. (p. 18)



Munsey, Paleocene Ostracoda from Alabama



Munsey, Paleocene Ostracoda from Alabama

Occurrence.—Rare in the Coal Bluff.

Remarks.—Although this unusual species lacks the quadrate shape of *Cytherelloidea* and is remarkably similar to *Morrowina excavata* (Alexander), having the same outline, surface punctae, and depression, the presence of the ventral ridge apparently places it in the genus *Cytherelloidea*.

Genus PLATELLA Coryell & Fields, 1937

Platella CORYELL & FIELDS, 1937, Amer. Mus. Nat. Hist. Nov., no. 956, p. 3.

Type species: *Platella gatunensis* Coryell & Fields, 1937, Amer. Mus. Nat. Hist. Nov., no. 956, p. 3, figs. 2a, 2b.

Description.—Carapace small, thin-shelled, subrectangular. Thickest near the posterior. Dorsal margin straight to very gently convex; anterior evenly rounded; venter straight to slightly sinuate in middle portion; posterior rounded, smaller than anterior. Right valve larger than the left, overlapping at the dorsal and ventral margins. Entire surface covered by numerous, large reticulations, tending to be crudely aligned with the long axis of the carapace, especially near the dorsal and ventral margins. A shallow sulcus is located in the center of the carapace just dorsal from the middle. Hinge simple, consisting of a shallow groove in the right valve into which fits the left. On the interior a very narrow marginal area is visible at the anterior end.

Coryell and Fields described the muscle scar of the Miocene species as being composed of "four groups." The Midway species shows a scar pattern more typical of the family Cytherellidae, being composed of nine small, irregularly shaped elements, the over-all outline more or less ovate, with the individual elements crudely aligned in two nearly vertical rows, four scars to a row and both topped by a smaller, indistinct scar. As contrasted with the Coal Bluff *Cytherella* muscle scar, *Platella* has a smaller, more rounded pattern, the individual scars being smaller, less regularly arranged, more consistent in size, and more irregularly shaped.

PLATELLA KELLETTAE Munsey, n. sp.
Plate 1, figure 4

Description.—Carapace small, elongate, subrectangular, thin-shelled. Thickest quite near the posterior. Dorsal margin straight to very gently convex; anterior almost evenly rounded; ventral margin gently concave slightly in front of the middle; posterior more narrowly rounded than the anterior, and sloping more gently at the postdorsal than at the postventral angle. Shallow, median sulcus dorsal to middle, corresponding in position to the muscle scar area on the interior of the valve. Entire surface covered by large, very well-defined reticulations, those near the edges of the carapace tending to be aligned parallel to the margins. Muscle scar that described for Midway species. Other internal features typical of genus.

Dimensions of figured specimen.—Length .52 mm., height .26 mm.

Holotype.—AMNH (left valve) OT-110.

Occurrence.—Very rare in the Coal Bluff, only one specimen, a left valve, being found.

Remarks.—In addition to the differences in the muscle scar pattern, this species dif-

EXPLANATION OF PLATE 2

FIGS. *1, 2—Leguminocythereis parallelokladia* Munsey, n. sp. *1*, left valve, ×60. *2*, right valve, ×60. (p. 12)

3–7—Cytheropteron (*Cytheropteron*) *hincheyi* Munsey, n. sp. *3*, female, left valve, ×50. *4*, male, left valve, ×58. *5*, female, right valve, ×58. *6, 7*, young, right valves, ×50. (p. 16)

8, 9—Eucytherura latebrosa Weingeist. *8*, right valve, ×64. *9*, left valve, ×64. (p. 19)

10–13—Clithrocytheridea alexanderi Stephenson. *10*, left valve, ×60. *11*, right valve, ×58. *12*, young, right valve, ×60. *13*, young, left valve, ×60. (p. 14)

14–18—Clithrocytheridea ruida (Alexander). *14*, dorsal view, ×57. *15*, right valve, ×57. *16*, left valve, ×60. *17*, young, right valve, ×60. *18*, young, left valve, ×60. (p. 15)

19—Cytherura boldi Munsey, n. sp. Right valve, ×55. (p. 18)

20–22—Clithrocytheridea jessupensis (Howe & Garrett). *20*, dorsal view, ×60. *21*, right valve, ×60. *22*, left valve, ×60. (p. 14)

23—Haplocytheridea leei (Howe & Garrett). Left valve, ×58. (p. 14)

24—Brachycythere striatopunctata (Roemer). Right valve, ×48. (p. 11)

25—Haplocytheridea ? sp. Right valve, ×60. (p. 14)

26–27—Toulminia hyalokystis Munsey, n. gen., n. sp. *26*, dorsal view, ×55. *27*, right valve, ×55. (p. 7)

fers from *P. gatunensis* in being much more elongate in side view and more convex in dorsal outline. This species is named in honor of Mrs. Betty Kellett Nadeau.

Suborder PODOCOPA Sars, 1865 (1866)
Family BAIRDIIDAE Sars, 1865 (1866)
Genus BAIRDIA M'Coy, 1844

Bairdia M'COY, 1844, Synopsis Char. Carb. Fossils, Ireland, p. 164.
Bairdia KELLETT, 1934, Jour. Paleontology, vol. 8, pp. 120–138.
Bairdia (scar pattern), SCOTT, 1944, Jour. Paleontology, vol. 18, pp. 162–171.
Bairdia EDWARDS, 1944, Jour. Paleontology, vol. 18, p. 506.
Bairdia SYLVESTER-BRADLEY, 1950, Ann. and Mag. Nat. Hist., ser. 12, vol. 3, pp. 751–756, text figs. 1–5.

Type species: *Bairdia curta* M'Coy, 1844, Synopsis Char. Carb. Fossils, Ireland, p. 164.

BAIRDIA sp.
Plate 3, figures 15, 16

One adult and a few broken early molts of *Bairdia* were found in the Coal Bluff material, but the preservation was such that no further attempt at identification was made.

Family CYTHERIDAE Baird, 1850
Subfamily CYTHERINAE Dana, 1852
Genus CYTHEROMORPHA Hirschmann, 1909

Cytheromorpha HIRSCHMANN, 1909, Meddelanden Soc. pro Fauna Flora Fennica, pp. 290–292.
Cytheromorpha HIRSCHMANN, 1912, Acta Soc. Fauna Flora Fennica, vol. 36, pp. 43–44.
Cytheromorpha SARS, 1922–28, Acc. Crustacea Norway, vol. 9, p. 177.
Cytheromorpha ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 222–223.

Type species: *Cythere fuscata* Brady, 1869, Ann. Mag. Nat. Hist., ser. 4, vol. 3, p. 47, pl. 7, figs. 5–8. Syn. *Cythere drammensis* Sars, 1869, *Cythere albula* Hirschmann, 1909.

CYTHEROMORPHA SCROBICULATA
Alexander, 1934
Plate 3, figures 11–14

Cytheromorpha scrobiculata ALEXANDER, 1934, Jour. Paleontology, vol. 8, p. 223, pl. 32, fig. 19.
Cytheromorpha scrobiculata KLINE, 1943, Mississippi Geol. Surv., Bull. 53, p. 69, pl. 8, fig. 8.
Cytheromorpha scrobiculata HARRIS & JOBE, 1951, Microfauna Midway Ark., p. 72, pl. 13, fig. 5.

Remarks.—The Coal Bluff specimens show extreme dimorphism. The males are much more narrow and elongate than are the females. The carapace of the female is heavier, much shorter and broader, and possesses a decidedly more pointed posterior.

Dimensions of figured specimens.—Female, right valve, length .38 mm., height .21 mm., left valve, length .37 mm., height .18 mm.

Hypotype.—AMNH (double valve) OT-111.

Occurrence.—Common in the Coal Bluff at Caledonia. Reported as rare in the Wills Point and Kincaid formations of Texas, and very rare in the Porters Creek and Clayton formations of Mississippi. According to Harris and Jobe, it appears in most Arkansas Midway samples.

Genus TOULMINIA Munsey, n. gen.

Type species: *Toulminia hyalokystis* Munsey, n. sp.

Description.—Carapace small, compressed, quadrangular to subrhomboidal, highest near anterodorsal angle, thickest slightly posterior to middle. Dorsal margin straight; anterior obliquely rounded; ventral margin sinuate, converging posteriorly toward the dorsal margin; posterior straight, nearly at right angle to dorsal margin. Anterior and posterior edges may carry short, indistinct teeth. Surface heavily ornamented.

Hinge of right valve consists of small ovate anterior and posterior teeth, connected by a minutely crenulate groove. Immediately behind the anterior tooth, and in front of the posterior tooth, the dorsal groove widens, forming small, shallow, oval-shaped sockets. Hinge in left valve consists of small anterior and posterior sockets, connected by a narrow dorsal bar. Just anterior to the posterior socket, the bar swells into a low, elongate tooth; the tooth posterior to the anterior socket is shorter and more narrow than that on the posterior.

Inner margin coincides with the line of concrescence except at the anterior and posterior ends, being broader at the anterior, and deviating only slightly from the line of concrescence at the posterior. Radial pore canals indistinct. The muscle scar is largely obscured by surface ornamentation, but appears to consist of four small, vertically aligned scars, anterior to which is a larger element with a more questionable one dorsal to this. Female differs from male in being less elongate, slightly less compressed, and in having a gently arched dorsal margin.

This genus is named in honor of Dr. Lyman D. Toulmin of Florida State University, Tallahassee, Florida.

TOULMINIA HYALOKYSTIS Munsey, n. sp.
Plate 2, figures 26–27; text figure 1

Description.—Carapace minute, somewhat compressed, subrhomboidal, highest at anterodorsal angle, thickest slightly behind middle. Dorsal margin straight; anterior obliquely rounded; ventral margin sinuate, converging posteriorly toward the dorsal margin; posterior nearly straight, almost perpendicular to dorsal margin. Anterior edge usually carries three or four very short, blunt spines; the posterior rim exhibits two or three very indistinct spines. Surface very heavily ornamented with heavy, broad ridges which have short, more or less distinct lateral extensions. A high, prominent marginal rim, with an inner bordering depression, circumscribes the periphery of the carapace; this rim is especially high around the anterior edge. The most prominent ridge originates at the marginal rim posterior to the middle of the ventral margin, extends very slightly below the venter, one short segment curving abruptly upward and posteriorly, dying out after extending a very short distance; the other segment extends upward and anteriorly, branching out into several smaller segments near the anterior half of the carapace. Another ridge begins at the anteroventral angle, extends parallel to the ventral marginal ridge, and joins the prominent ventral ridge just dorsal to its highest point. A pronounced, rounded ridge originates at the marginal rim near the middle of the hinge line, extends posteriorly parallel to, and away from, the marginal rim, bending almost vertically downward just short of the postdorsal angle and dies out near the longitudinal axis of the carapace. Anterior to this, and at the widest portion of the carapace, is a short, high, irregular ridge with several low, irregular extensions. Obscured by the numerous ridges are rather large and heavy reticulations. Internal features those described for genus.

Female differs from the male in being less elongate, slightly less compressed, and in having a gently arched dorsal margin. Although very abundant, all specimens were approximately the same size, no young being distinguishable

Dimensions of figured specimens.—Double valve, length .34 mm., width .16 mm., height .18 mm. Right valve, length .35 mm., height .18 mm.

Holotype.—AMNH (right valve) OT-112;

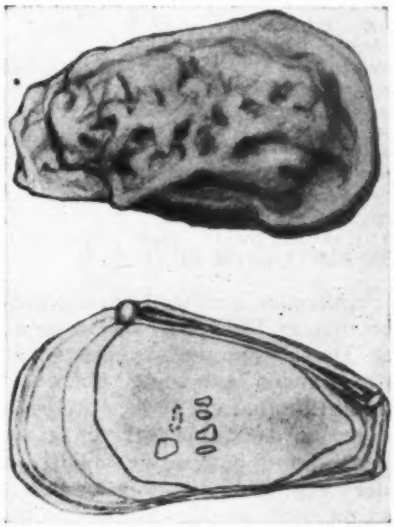


FIG. *1*—External and internal view, right valve, of *Toulminia hyalokystis* Munsey, n. gen., n. sp. ×140.

paratype (left valve) OT-113; paratype (double valve) OT-114.

Occurrence.—Abundant in the Coal Bluff at Caledonia. The author has seen specimens from the Clayton and Nanafalia formations of Alabama.

Subfamily TRACHYLEBERINAE Sylvester-Bradley, 1948
Genus CYTHEREIS Jones, 1849

Cythereis JONES, 1849, Mon. Entom. Cret. England, Palaeont. Soc. London, p. 19.
Cythereis ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 218–219.
Archicythereis HOWE (part), 1936, Louisiana Dept. Cons., Geol. Bull. 7, p. 57.
Cythereis EDWARDS, 1944, Jour. Paleontology, vol. 18, p. 521.
Cythereis VAN DEN BOLD, 1946, Cont. Study Ostracoda, p. 29.
Cythereis STEPHENSON, 1946, Jour. Paleontology, vol. 20, p. 334.
Trachyleberis SYLVESTER-BRADLEY, 1948 (non Brady, 1898), Jour. Paleontology, vol. 22, pp. 792–797.

Type species: *Cytherina ornatissima* (Reuss), 1845, Verst. Boh. Kreide.

CYTHEREIS BASSLERI Ulrich, 1901
Plate 4, figures 6, 7, 12–14

Cythereis bassleri ULRICH, 1901, Maryland Geol. Surv., Eocene vol., p. 120, pl. 16, figs. 19–21.
Cythereis bassleri WELLER, 1907, Geol. Surv. New Jersey, Paleontology, vol. 4, p. 843, pl. 110, figs. 1–3.
Cythereis bassleri CUSHMAN, 1925, Bull. Am. Assoc. Petrol. Geol., vol. 9, p. 302, pl. 8, figs. 3a–3c.
Cythereis bassleri ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 219–220.
Cythereis bassleri JENNINGS, 1936, Bull. Am. Paleont., vol. 23, no. 78, p. 51, pl. 7, figs. 1a–1b.
Cythereis bassleri VAN DEN BOLD, 1946, Cont. Study Ost., p. 94, pl. 6, fig. 20.
Cythereis bassleri SCHMIDT, 1948, Jour. Paleontology, vol. 22, pp. 422–423, pl. 64, fig. 13.
Cythereis bassleri SWAIN, 1948, Maryland Geol. Surv., Bull. 2, p. 197, pl. 13, fig. 7.

Description.—Carapace heavy, oblong to subrectangular, highest at anterodorsal angle. Dorsal margin straight; anterior broadly rounded, extending somewhat below the ventral margin at the anteroventral angle; ventral margin slightly sinuate, subparalleling, and converging slightly with the dorsal margin; posterior end slightly convex on lower portion, concave on upper. Anterior margin carries numerous small spines, posterior four to six short, blunt spines. High subcentral node. Prominent glassy eyespot at the anterodorsal angle. Heavy thick marginal rim circumscribes the entire periphery of the carapace, being most pronounced at the anterior. A depression borders the marginal rim. The posterior end of the valves carries a prominent, nearly vertical ridge which extends posteriorly from both ends, the ventral extension curving gently downward, terminating at the anteroventral angle. The dorsal extension subparallels the dorsal margin for about two-thirds its length before turning downward and backward to the subcentral node, where it again curves, extending anteriorly parallel to the ventral margin, dying out just before reaching the anterior marginal rim. Just below, and parallel to this ridge is another, which begins at the node and dies out at about the same spot. Another prominent ridge extends from the node to the eyespot. In most specimens a median, longitudinal ridge extends posteriorly from the node to join the posterior ridge. A few specimens show a faint, irregular ridge originating at the juncture of the ventral and posterior ridges, and extending to the node. Surface coarsely reticulate. The more delicate posterior end of the larger left valve is more blunt than that of the right. The young have a more delicate and angular carapace, the angles formed by the posterior intersections of the ridges being produced into sharp, well-defined spines which are more pronounced at the postventral angle. Even in the youngest molts the main ridges are prominent and occur in the same pattern as do those of the adults.

Hingement typical for the genus. Radial pore canals numerous, somewhat irregular. Muscle scar obscured by surface ornamentation.

Dimensions of figured specimens.—Adult, left valve, length .61 mm., height .35 mm., right valve (fig. 12), length .71 mm., height .38 mm. (fig. 14), length .58 mm., height .29 mm. Young, right valve, length .56 mm., height .28 mm., left valve, length .51 mm., height .28 mm.

Hypotype.—AMNH (left valve) OT-115; (right valve) OT-116.

Occurrence.—Rather common in the Coal Bluff at Caledonia. Ulrich, as well as Schmidt, describes this species from the Aquia formation (lower Wilcox) of Maryland; Swain from well cuttings of probable lower Eocene age from Maryland; Weller from the Vincentown (lower Eocene) of New Jersey; Jennings from the Mount Laurel and Navesink formations (Upper Cretaceous) of New Jersey. Cushman reported it in Eocene strata of Mexico, and Van den Bold from the Paleocene and lower Eocene of Guatemala and British Honduras.

Remarks.—Even in specimens occurring at the same locality, this species varies somewhat in surface ornamentation. Some of the Coal Bluff specimens (plate 4, figs. 6 and 7) are questionably placed with this species, being either young or merely showing some of the many variations in ornamentation exhibited by this species.

CYTHEREIS PRESTWICHIANA
Jones & Sherborn, 1887
Plate 4, figures 3–5

Cythereis prestwichiana JONES & SHERBORN, 1887, Geol. Mag., p. 454, pl. 11, figs. 11a–11b.
Cythereis prestwichiana JONES & SHERBORN, 1889, Suppl. Mon. Tert. Entom. England, Palaeont. Soc. London, p. 33, pl. 2, figs. 13, 14.
Cythereis prestwichiana ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 220–221, pl. 32, figs. 14–15.

Cythereis prestwichiana KLINE, 1943, Mississippi Geol. Surv., Bull. 53, p. 68, pl. 8, fig. 11.
Cythereis prestwichiana VAN DEN BOLD, 1946, Cont. Study Ostracoda, p. 94, pl. 11, fig. 2.
Cythereis prestwichiana HARRIS & JOBE, 1951, Microfauna Midway Ark., pp. 71–72, pl. 13, fig. 3.

Dimensions of figured specimens.—Double valve, length .56 mm., width .21 mm., height .28 mm. Right valve, length .55 mm., height .28 mm. Left valve, length .55 mm., height .30 mm.

Hypotype.—AMNH (double valve) OT-117.

Occurrence.—Very common in the Coal Bluff. Alexander reports it to be abundant in the Kincaid and Wills Point formations of Texas; Kline found it to be fairly common in the Clayton and Porters Creek formations of Mississippi. Kellett and Echols (unpublished manuscript) found a species which apparently belongs with this from the Bashi marl member of the Hatchetigbee formation (upper Wilcox) of Alabama. Van den Bold describes it from the Paleocene strata of Guatemala. Toulmin (1940, range chart) lists it from the Nanafalia (lower Wilcox) formation of Alabama. Harris and Jobe found it to be abundant in Arkansas Midway samples.

CYTHEREIS DICTYOLOBUS Munsey, n. sp.
Plate 4, figures 9–11

Description.—Carapace elongate, subclavate, much higher at anterior, thickest just anterior to middle. Dorsal margin nearly straight; anterior obliquely rounded, projecting below venter at anteroventral angle; ventral margin concave in center. Posterior of right valve convex on ventral half, concave on dorsum; posterior of left valve almost evenly rounded. Anterior rim finely denticulate; posterior edge possesses a few short, blunt teeth on ventral half. A very low and obscure subcentral node is present. A very narrow, smooth, obscure marginal rim borders the anterior and posterior ends. Posterior also possesses a rounded ridge parallel to the marginal rim and separated from it by a low shallow depression. Entire surface covered by very coarse and heavy reticulations, those near the anterior roughly aligned, forming ridges parallel to the anterior margin; on the posterior the ridges are less well arranged, and show no orderly arrangement near the center.

Only a few adult specimens were found, the hinge preservation of these being poor, but the hinge appears to consist, in the right valve, of a low, pointed anterior tooth, postjacent socket, groove, and small oval posterior tooth. Left valve apparently complement of right. The more numerous and better preserved young show typical hingement for young *Cythereis*. Muscle scar obscured. Inner marginal area fairly broad at anterior and posterior ends. Radial pore canals rather numerous, irregular.

Dimensions of figured specimens.—Left valve (fig. 9), length .58 mm., height .29 mm. (fig. 11), length .58 mm., height .26 mm. Right valve, length .58 mm., height .29 mm.

Holotype.—AMNH (left valve) OT-118; paratype (right valve) OT-119.

Occurrence.—Somewhat rare.

CYTHEREIS RETICULODACYI Swain, 1948
Plate 4, figures 1, 2, 8, 15, 16

Cythereis reticulodacyi SWAIN, 1948, Maryland Geol. Surv., Bull. 2, p. 202, pl. 13, figs. 13–14.

Dimensions of figured specimens.—Male, right valve, length .76 mm., height .38 mm., left valve, length .71 mm., height .38 mm. Young, without spines, length .59 mm., height .31 mm. Young, spinose, right valve, length .56 mm., height .30 mm., left valve, length .59 mm., height .32 mm.

Hypotype.—AMNH (left valve) OT-120; (right valve) OT-121.

Occurrence.—Common in the Coal Bluff. Swain describes it as rare in Eocene well cuttings from Maryland.

Remarks.—Some questionable forms occur which may be young molts of this species (plate 4, figs. 2, 8, 16). The simple hingement, narrow marginal area, and thin character of the carapace seem to be typical of early molts of ostracodes. The surface ornamentation appears to fit that of the adult forms although some specimens lack the heavily spinose surface, possibly due to abrasion (plate 4, fig. 2). These small forms are probably similar to "*Archycythereis*" *retiplana* Schmidt, *Cythereis deusseni* Howe and Chambers, and *Cythereis russelli* Howe and Garrett. Blake (1950) recognized a similar form as being the young of *Trachyleberis washburni* Blake. The author has recognized similar forms in the Clayton, Porters Creek, Nanafalia, and Hatchetig-

bee formations of Alabama, and believes them to be young of adult *Cythereis* with which they occur.

CYTHEREIS ABRARMUS Munsey, n. sp.
Plate 4, figure 21

Description.—Carapace elongate, subrectangular. Dorsal margin straight; anterior obliquely rounded, extending slightly below the ventral margin; ventral margin gently concave; posterior bluntly triangulate. Anterior rim finely denticulate; lower portion of posterior margin exhibits three or four short, blunt spines. Low, subcentral node present. Small, glassy eyespot at anterodorsal angle. Except on the dorsal edge, a heavy, rounded marginal rim circumscribes the periphery of the carapace. From the postventral angle a transverse posterior ridge extends anteriorly, subparalleling the ventral margin, and terminates at the anteroventral angle. Entire surface covered by heavy, deep, irregularly arranged reticulations. Although internal features are obscure, the hingement appears to be that of *Cythereis*.

Dimensions of figured specimen.—Length .59 mm., height .29 mm.

Holotype.—AMNH (left valve) OT-122.

Occurrence.—Very rare in the Coal Bluff.

GENUS PLATYCYTHEREIS Triebel, 1940

Platycythereis TRIEBEL, 1940, Senck., vol. 22, pp. 214–215.

Type species: *Cythereis excavata* Chapman and Sherborn, 1893, Geol. Mag., vol. 10, p. 348, pl. 14, fig. 8.

Description.—This genus has been separated from *Cythereis* by the very compressed nature of the carapace, the absence of a subcentral node, and by very heavy dentitions on the anterior margin. The carapace is strongly compressed, subrhomboidal, highest near the anterior. Dorsal margin straight; anterior rounded; ventral margin straight to concave in middle portion; posterior pointed. Anterior edge of carapace bears several heavy, lobate, somewhat flattened marginal teeth; posterior dentitions less well pronounced. No subcentral node present. Surface reticulate, ridged, usually possessing marked marginal rim. Eyespot usually present. Hinge in right valve consists of an elevated anterior tooth, postjacent socket and groove, and terminal posterior tooth. Hinge of left valve consists of an anterior socket, postjacent elevated tooth and ridge with a terminal posterior socket. Inner margin and line of concrescence coincide. Radial pore canals rather numerous, fairly straight. Muscle scar appears to consist of a vertical row of four scars with a single scar anterior to them. As in *Cythereis*, the males are more elongate than the females. The young do not appear as thin-shelled as those of *Cythereis*, but are more so than the adults of *Platycythereis*. The heavy anterior dentitions are lacking in the young, but carry the same heavy reticulations as the adults. On young specimens the juncture of the ridges appears to produce sharp spines, especially on the postdorsal portion of the carapace.

PLATYCYTHEREIS CANCELLOSA
(Alexander), 1934
Plate 4, figures 17–20

Cythereis cancellosa ALEXANDER, 1934, Jour. Paleontology, vol. 8, p. 221, pl. 32, fig. 10.
Cythereis cancellosa VAN DEN BOLD, 1946, Cont. Study Ostracoda, p. 95, pl. 11, fig. 1; pl. 6, fig. 14.

Dimensions of figured specimens.—Double valve, length .67 mm., width .22 mm. Adult, left valve, length .65 mm., height .31 mm. Young (fig. 19), right valve, length .54 mm., height .28 mm. Young (fig. 20), right valve, length .47 mm., height .24 mm.

Hypotype.—AMNH (double valve) OT-123.

Occurrence.—Common in the Coal Bluff. Rare in the Kincaid and Wills Point formations of Texas. The author has found it to be rather common in the Nanafalia formation of Alabama. Van den Bold reports the species from the Upper Cretaceous, Paleocene, and lower Eocene of Guatemala and British Honduras; in Cuba from the lower Eocene. Van den Bold also found this species in the Miocene of Guatemala but suspects it to be from reworked material.

Genus BRACHYCYTHERE Alexander, 1933

Brachycythere ALEXANDER, 1933, Jour. Paleontology, vol. 7, p. 204.
Brachycythere MURRAY & HUSSEY, 1942, Jour. Paleontology, vol. 16, pp. 164–182.
Brachycythere STEPHENSON, 1946, Jour. Paleontology, vol. 20, pp. 331–332, 306–307.

Type species: *Cythere sphenoides* Reuss, 1854, Kais. Akad. Wissen. Wien, Denkschr., vol. 7, p. 141, pl. 26, fig. 2.

Description.—Carapace subquadrangular to ovate. Dorsal margin arched; anterior broadly and obliquely rounded; ventral margin convex; posterior compressed, subrounded. Highest at anterior, inflated ventrally, often with ventral alate process. Left valve larger than right, overlapping along the dorsal edge. Ends sometimes spinose. Surface of the type species smooth, but other forms referred to this genus exhibit punctae, reticulations, ridges and pits.

Hinge in the left valve consists of an anterior socket and postjacent tooth connected to a posterior crenulate socket by a bar lying well below the dorsal margin. In the right valve a prominent knob-like anterior tooth and postjacent socket are connected by a groove to the posterior notched, elongate tooth. At the posterior end of the right valve of some species lies an internal, shallow elongate socket, and below this a groove with numerous, small crenulations extending around the postventral portion of the valve. This portion of the left valve is the complement of the right. The hinge of the young shows an elongate, crenulate ridge on the anterior of the right valve, corresponding in position to the very pronounced tooth of the adult form; the crenulate dorsal groove extends the full length of the hinge line, replacing the postjacent socket exhibited in the adults, and extends over the anterior crenulate ridge before terminating. The posterior crenulate ridge of the right valve is carried through all stages of development, being much more pronounced in the adult form. As in the adults, the hinge of the left valve is the complement of the right.

Marginal area broad, the inner margin and the line of concrescence coinciding throughout. Radial pore canals numerous, somewhat irregular. Muscle scar varies somewhat in the alignment of four vertical scars; anterior to this row are two other scars. See Alexander (1933, p. 185) for illustrations of muscle scar.

BRACHYCYTHERE PLENA
Alexander, 1934
Plate 3, figures 17–21

Brachycythere plena ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 216–217, pl. 33, fig. 6.
Brachycythere plena MURRAY & HUSSEY, 1942, Jour. Paleontology, vol. 16, p. 176, pl. 27, figs. 2, 5, 6; text fig. 2, figs. 3, 7.
Brachycythere plena KLINE, 1943, Mississippi Geol. Surv., Bull. 53, pp. 67–68, pl. 8, fig. 3.
Brachycythere plena VAN DEN BOLD, 1946, Cont. Study Ostracoda, p. 108, pl. 13, figs. 4–5.
Brachycythere plena HARRIS & JOBE, 1951, Microfauna Midway Ark., p. 71, pl. 12, fig. 6.

Remarks.—Dimorphism marked. The female is much more bulbous and rounded than the male, with the result that the "crescent-shaped depression" is much deeper and more evident in the male. In addition, the "ventro-lateral ridges" are much more pronounced in the male. Surface of the youngest molts smooth, becoming more punctate as the shell increases in size. A very few specimens, both young and adult carry a short spine on the posterior portion of the alate structure. The male as denoted here may be the same as *Brachycythere plena tschoppi* Van den Bold, described as having a strongly flattened alar border.

Dimensions of figured specimens.—Double valve, female, length .96 mm., width .58 mm. Female, right valve, length .91 mm., height .50 mm., left valve, length .91 mm., height .59 mm. Male, right valve, length .91 mm., height .56 mm. Young, length .79 mm., height .46 mm.

Hypotype.—AMNH (left valve) OT-124; (right valve) OT-125.

BRACHYCYTHERE STRIATOPUNCTATA
(Roemer), 1838
Plate 2, figure 24

Cytherina striatopunctata ROEMER, 1838, Neues Jahrb. Min., p. 515, pl. 6, fig. 3.
Cythere striatopunctata BOSQUET, 1852, Mem. Couron. Acad. Belg., vol. 24, p. 62, pl. 3, fig. 1.
Cythere striatopunctata JONES, 1856, Mon. Tert. Entom. England, Palaeont. Soc. London, p. 27, pl. 5, fig. 6, 7a–7b, 10.
Cythere striatopunctata EGGER, 1858, Neues Jahrb. Min., pp. 422, 441, pl. 17, figs. 9a–9d.
Cythere striatopunctata JONES & SHERBORN, 1889, Suppl. Mon. Tert. Entom. England, Palaeont. Soc. London, p. 19.
Cythere striatopunctata HEJJAS, 1892, Ertesito. 2, Nat. Abtheil., vol. 15, part 2, pp. 159, 164, 330.
Cythere striatopunctata LIENENKLAUS, 1894, Zeitschr. Deutschen Geol. Ges., vol. 46, p. 181.
Cythere striatopunctata LIENENKLAUS, 1896, K. Bayerische Akad. Wissen., Munich, Math.-Phy.-Classe-Sitzung., p. 189.
Cythere striatopunctata SCHACKO, 1896, Archiv. Ver Freunde Nat. Mecklenburg, vol. 50, p. 325.
Cythere striatopunctata CAPEDER, 1902, R. Accad. delle Sci. Torino, p. 14, figs. 28a–28b.
Cythere striatopunctata ULRICH & BASSLER, 1904, Maryland Geol. Surv., Miocene vol., p. 99.
Cythere striatopunctata CHAPMAN, 1911, Quart. Jour. Geol. Soc. London, vol. 67, p. 661.

Description.—Carapace elongate, subrectangular, rounded. Dorsal margin straight to evenly convex; anterior obliquely rounded; ventral margin strongly convex; posterior slightly truncated, somewhat compressed, bearing three to four spines. Obscure, elongate eyespot at anterodorsal angle. Surface covered by rounded, prominent longitudinal ridges, curving upward near the ventral and downward near the dorsal margin; those in the center show little curvature. Large, deep reticulations lie in the grooves between the ridges. Hingement typical for genus. Muscle scar obscured by surface ornamentation. The young appear to be less angular than the adults, especially at the posterior end; the young also show a narrow inner marginal area.

Dimensions of figured specimen.—Length .82 mm., height .44 mm.

Hypotype.—AMNH (left valve) OT-126.

Occurrence.—Rare in the Coal Bluff. It has been reported from a number of Tertiary beds, both upper and lower, from several European countries.

Genus LEGUMINOCYTHEREIS Howe, 1936

Leguminocythereis HOWE, 1936, Louisiana Dept. Cons., Geol. Bull. 7, p. 61.

Type species: *Leguminocythereis scarabeus* Howe and Law, 1936, Louisiana Dept. Cons., Geol. Bull. 7, pp. 61–62, pl. 4, figs. 12, 17; pl. 5, figs. 15–17.

LEGUMINOCYTHEREIS PARALLELOKLADIA Munsey, n. sp.
Plate 2, figures 1, 2

Description.—Carapace rather heavy, oblong-subquadrate, highest near anterior, thickest near posterior. Dorsal margin nearly straight, slightly concave near middle of hinge line; anterior margin obliquely rounded; ventral margin gently concave near anterior; posterior end compressed near edge, bluntly rounded on left valve, slightly pointed near median line on right. Anterior margin bears ten to twelve obscure, short spines; posterior margin exhibits two or three very short, blunt teeth. Low eyespot present at anterodorsal angle. Surface very heavily ornamented. Subdued swelling or node just anterior to middle. A heavy marginal rim originates at eyespot, extends around anterior, ventral and posterior margins. A second, parallel ridge is separated from the marginal rim by a shallow depression. A third prominent ridge begins near the middle of the ventral margin just above the second ridge, the two being separated by a pronounced depression. This third ridge extends anteriorly parallel to the ventral margin, curves obliquely upward and backward, and protrudes over the dorsal margin near the postdorsal angle where it curves almost vertically downward before dying out near the long axis of the carapace. Approximately three lesser ridges extend anteriorly and posteriorly from the node, giving a web-like pattern to the ornamentation. Very heavy and deep reticulations occur between all ridges. Although poorly preserved, the hinge appears to consist in the right valve of an anterior, well elevated, pointed tooth, postjacent rounded socket extending posteriorly into a narrow groove, and a large, highly elevated posterior tooth. Hinge of left valve apparently complement of right. Males differ from fe-

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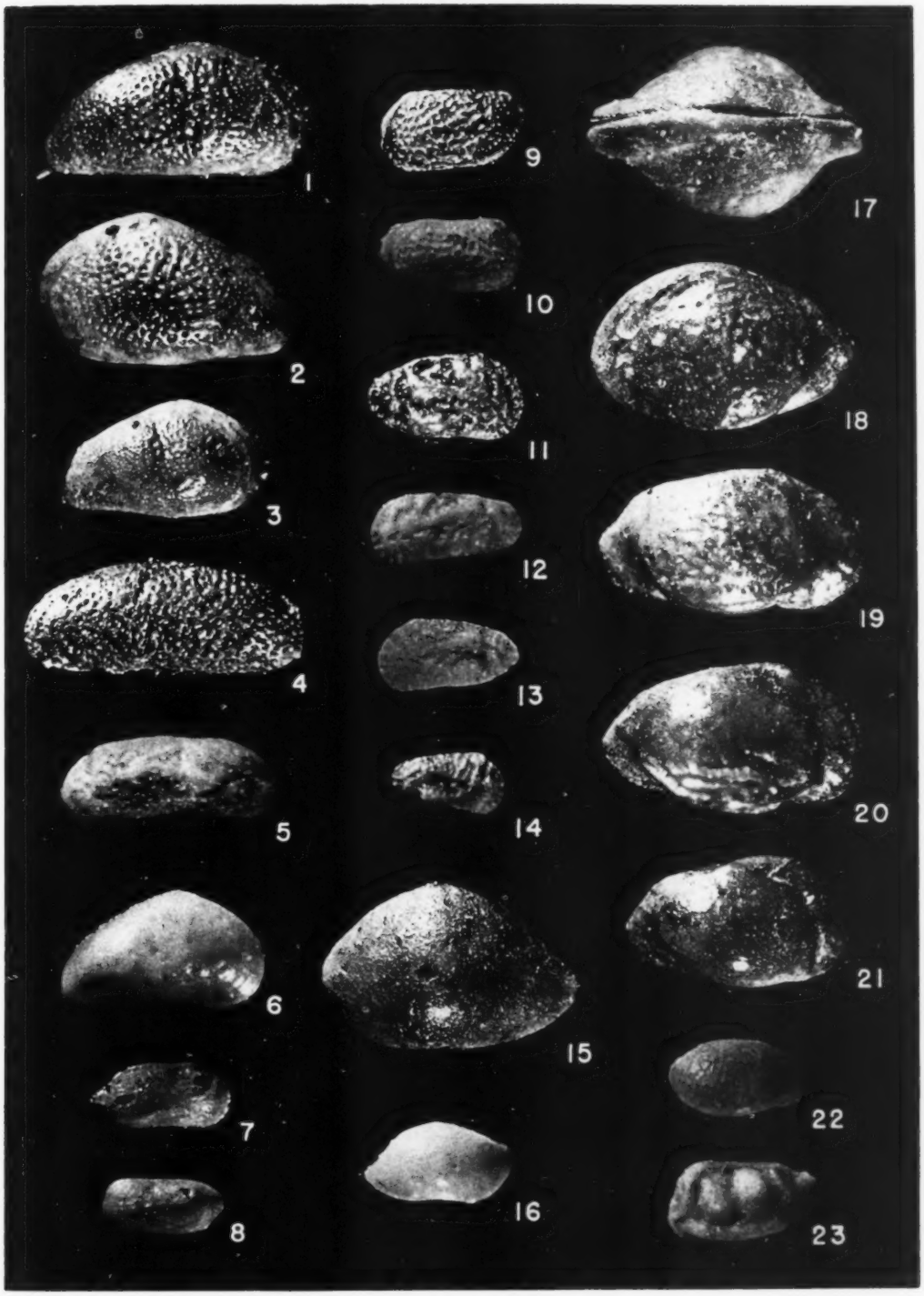
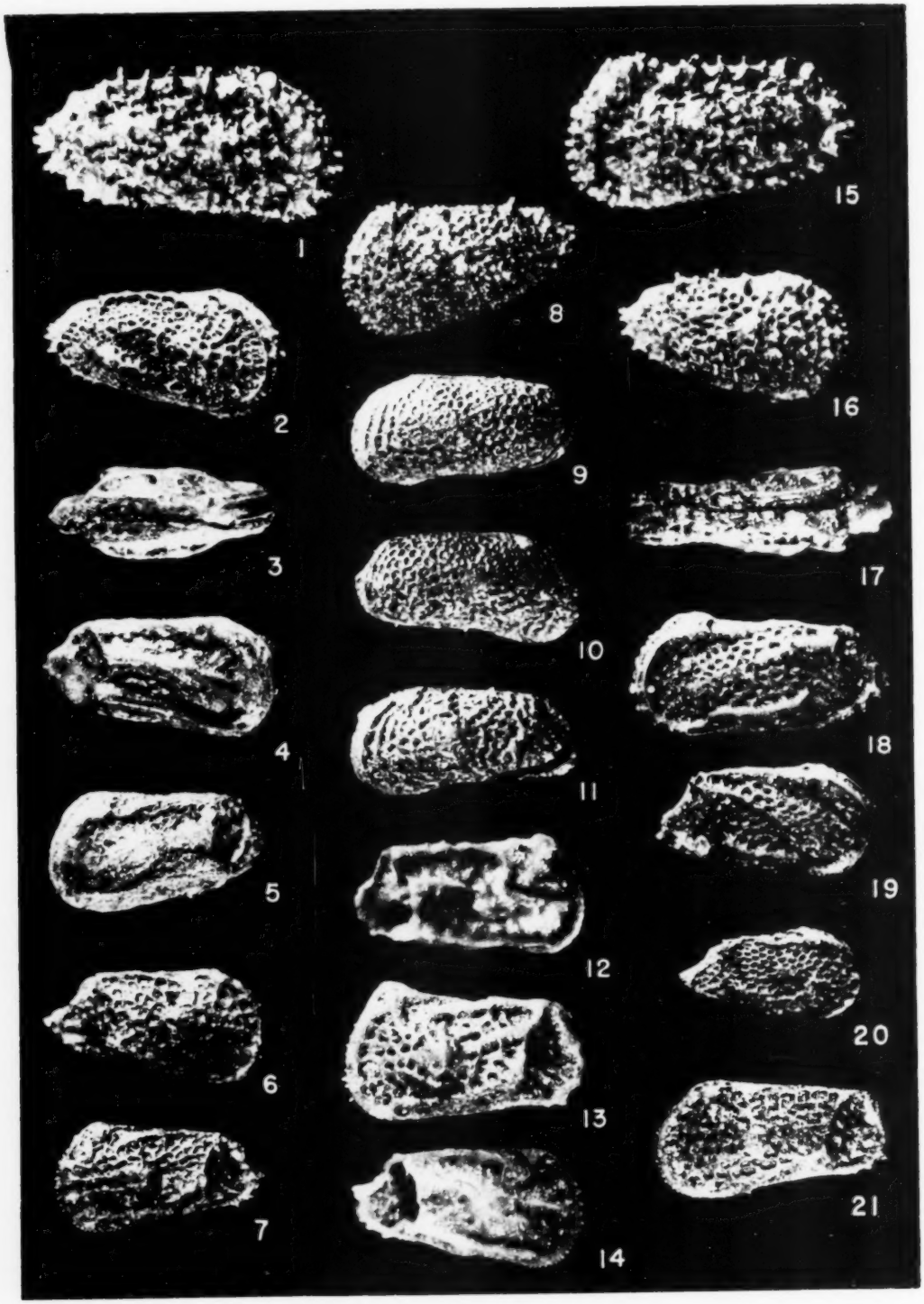
EXPLANATION OF PLATE 3

FIGS. *1–3—Clithrocytheridea macrolaccus* Munsey, n. sp. *1*, right valve, ×59. *2*, left valve, ×58. *3*, young, right valve, ×58. (p. 15)
4—Cytherideis mayeri (Howe & Garrett). Left valve, ×58. (p. 13)
5—Cytherideis caledoniensis Munsey, n. sp. Right valve, ×56. (p. 13)
6—Eucythere triordinis Schmidt. Right valve, ×54. (p. 15)
7—Cytherura dorilaemus Munsey, n. sp. Right valve, ×55. (p. 17)
8—Cytherura phaseous Munsey, n. sp. Left valve. ×55. (p. 18)
9, 10—Loxoconcha notoaulax Munsey, n. sp. *9*, left valve (darkened), ×59. *10*, right valve (undarkened), ×58. (p. 16)
11–14—Cytheromorpha scrobiculata Alexander. *11*, female, right valve, ×60. *12*, male, left valve, ×60. *13*, female, left valve, ×58. *14*, male, right valve, ×56.
15–16—Bairdia sp. *15*, adult, left valve. ×43. *16*, young, right valve, ×36. (p. 6)
17–21—Brachycythere plena Alexander. *17*, female, dorsal view, ×43. *18*, female, left valve, ×43. *19*, male, right valve, ×43. *20*, female, right valve, ×43. *21*, young, right valve, ×43. (p. 11)
22—Cytheropteron (*Cytheropteron*) *liogluma* Munsey, n. sp. Right valve. ×60. (p. 17)
23—Monoceratina biphysa Munsey, n. sp. Left valve, ×60. (p. 17)



Munsey, Paleocene Ostracoda from Alabama



Munsey, Paleocene Ostracoda from Alabama

males in being more elongate, somewhat compressed, and less inflated posteriorly.

Dimensions of figured specimens.—Left valve, length .53 mm., height .29 mm. Right valve, length .58 mm., height .27 mm.

Holotype.—AMNH (right valve) OT-127; paratype (left valve) OT-128.

Genus CYTHERIDEIS Jones, 1856

Cytherideis JONES, 1856, Tert. Entom. England, Palaeont. Soc. London, p. 46.

Type species: *Cythere botellina* Jones, 1870, new name for *Cythere* (*Cytherideis*) *flavida* Jones, 1856 (not *Cythere flavida* O.F. Müller, and not *Cytherideis subulata* Brady, 1868 which had been designated as the type species by Brady and Norman, 1889).

The exact taxonomic position of this genus is in doubt. Information concerning the type species was very kindly furnished by Dr. H. V. Howe, of Louisiana State University, who is now engaged in problems concerning this genus.

CYTHERIDEIS MAYERI (Howe & Garrett), 1934

Plate 3, figure 4

Bythocypris ? mayeri HOWE & GARRETT, 1934, Louisiana Dept. Cons., Geol. Bull. no. 4, p. 29, pl. 1, figs. 8–10.
Xestoleberis mayeri SCHMIDT, 1948, Jour. Paleontology, vol. 22, pp. 410–411, pl. 63, fig. 10; text fig. 2a.
Cytherideis mayeri BLAKE, 1950, Jour. Paleontology, vol. 24, p. 179.

Dimensions of figured specimen.—Length .71 mm., height .28 mm.

Hypotype.—AMNH (left valve) OT-129.

Occurrence.—Rather rare in the Coal Bluff. It has been recorded as rare in the Aquia formation of Maryland, and in the Sabine group at both Sabinetown, Louisiana and Nanafalia, Alabama.

CYTHERIDEIS CALEDONIENSIS Munsey, n. sp.

Plate 3, figure 5

Description.—Carapace heavy, elongate, subrectangular, highest posterior to middle. Dorsal margin nearly straight to unevenly arched; anterior narrowly and unevenly rounded, somewhat compressed, finely denticulate; ventral margin contracted near middle; posterior bluntly subacute, rimmed, compressed. Surface heavily reticulate. Anterior to the middle a deep, narrow sulcus bifurcates immediately below the dorsal edge, both segments trend slightly toward the anterior and terminate short of the center. A well-defined vertical ridge originates at the postdorsal angle, forms a right angle at the postventral angle and extends anteriorly for a short distance. Slightly below the sulcus and anterior to the middle a gently arched longitudinal ridge originates and extends posteriorly, terminating at the vertical posterior ridge. Two well-defined ridges begin near the anterior margin, curve downward and extend two-thirds the length of the carapace before terminating at the ventral margin. Muscle scar obscured, other internal features characteristic of genus.

Dimensions of figured specimen.—Length .58 mm., height .22 mm.

Holotype.—AMNH (right valve) OT-130.

Occurrence.—Very rare in the Coal Bluff.

Subfamily CYTHERIDEINAE Sars, 1925

Genus HAPLOCYTHERIDEA Stephenson, 1936

Cytheridea (*Haplocytheridea*) STEPHENSON, 1936, Jour. Paleontology, vol. 10, p. 700.
Cytheridea (*Leptocytheridea*) (part) STEPHENSON, 1937, Jour. Paleontology, vol. 11, p. 156.
Cytheridea (*Phractocytheridea*) SUTTON & WILLIAMS, 1939, Jour. Paleontology, vol. 13, p. 571.
Haplocytheridea STEPHENSON, 1946, Jour. Paleontology, vol. 20, pp. 321–322.

EXPLANATION OF PLATE 4

FIGS. *1, 2, 8, 15, 16*—*Cythereis reticulodacyi* Swain. *1*, male, right valve, ×60. *2*, young without spines, right valve, ×60. *8*, spinose young, left valve, ×60. *15*, male, left valve, ×60. *16*, spinose young, right valve, ×60. (p. 9)

3–5—*Cythereis prestwichiana* Jones and Sherborn. *3*, dorsal view, ×60. *4*, right valve, ×64. *5*, left valve, ×60. (p. 8)

6, 7—*Cythereis bassleri* ? Ulrich. *6*, right valve, ×60. *7*, left valve, ×60. (p. 8)

9–11—*Cythereis dictyolobus* Munsey, n. sp. *9*, left valve, ×58. *10*, right valve, ×58. *11*, left valve, ×58. (p. 9)

12, 13, 14—*Cythereis bassleri* Ulrich. *12*, right valve, ×48. *13*, left valve, ×60. *14*, right valve, ×60. (p. 8)

17–20—*Platycythereis cancellosa* (Alexander). *17*, dorsal view, ×60. *18*, adult, left valve, ×60. *19*, young, right valve, ×60. *20*, young, right valve, ×58. (p. 10)

21—*Cythereis abrarmus* Munsey, n. sp. Left valve, ×58. (p. 10)

Type species: *Cytheridea montgomeryensis* Howe and Chambers, 1935, Louisiana Dept. Cons., Geol. Bull. 5, pp. 17–18, pl. 1, fig. 1; pl. 2, figs. 1–3, 7, 9; pl. 6, figs. 17–18.

HAPLOCYTHERIDEA LEEI (Howe & Garrett), 1934
Plate 2, figure 23

Cytheridea leei HOWE & GARRETT, 1934, Louisiana Dept. Cons., Geol. Bull. 4, p. 33, pl. 1, figs. 22–23.
Cytheridea (*Haplocytheridea*) *leei* STEPHENSON, 1938, Jour. Paleontology, vol. 12, p. 572, pl. 67, figs. 4, 5; text figs. 1, 2.
Haplocytheridea leei SCHMIDT, 1948, Jour. Paleontology, vol. 22, p. 424, pl. 63, figs. 8, 9.

Description.—Carapace, heavy, elongate, subpyriform, highest anterior to middle. Dorsal margin arched, flattened along hinge line; anterior broadly and obliquely rounded, denticulate; ventral margin nearly straight, somewhat convex near the middle portion; posterior narrow, subacutely rounded, compressed. According to Stephenson (1938, p. 572), the surface ornamentation varies from smooth to pronouncedly pitted. The Coal Bluff specimens exhibit very marked pitting with irregular alignment producing low, rounded ridges parallel to the margins at the anterior and posterior ends, and three or four nearly vertical ridges near the center of the carapace. Stephenson describes the sexual dimorphism as being marked, the females differing from the males in being more broadly rounded, more strongly tumid, and having the hinge structure more heavily developed. The Coal Bluff specimens exhibit very well-developed crenulations in all elements of the hinge. Other internal features typical for the genus.

Dimensions of figured specimen.—Length .69 mm., height .42 mm.

Hypotype.—AMNH (left valve) OT-131.

Occurrence.—Rare in the Coal Bluff. Described as common in the Nanafalia formation in Louisiana and Alabama, and as common to rare in the Aquia formation of Virginia and Maryland.

HAPLOCYTHERIDEA? sp.
Plate 2, figure 25

Description.—Carapace small, triangularly ovate, highest anterior to middle. Dorsal margin nearly straight along hinge line, sloping gently toward posterior; anterior broadly and obliquely rounded; ventral margin straight to gently concave in middle portion. Posterior narrowly subacute, somewhat compressed. Widest near middle. A shallow, dorsal sulcus divides the valve into approximately two equal parts. Rather prominent rounded ridges parallel the outline of the carapace except near the middle where they curve downward around the shallow sulcus. The internal features are obscure, making identification difficult. This may be an early molt of another species.

Dimensions of figured specimen.—Length .50 mm., height .29 mm.

Hypotype.—AMNH (right valve) OT-132.

Occurrence.—Rare in the Coal Bluff.

Genus CLITHROCYTHERIDEA Stephenson, 1936

Cytheridea (*Clithrocytheridea*) STEPHENSON, 1936, Jour. Paleontology, vol. 10, p. 702.
Cytheridea (*Leptocytheridea*) (part) STEPHENSON, 1937, Jour. Paleontology, vol. 11, p. 156.
Clithrocytheridea STEPHENSON, 1944, Jour. Paleontology, vol. 18, p. 449.
Clithrocytheridea STEPHENSON, 1946, Jour. Paleontology, vol. 20, p. 326.

Type species: *Cytheridea ? garretti* Howe and Chambers, 1935, Louisiana Dept. Cons., Geol. Bull. 5, p. 14, pl. 1, figs. 4, 5; pl. 2, figs. 11, 12; pl. 6, figs. 10, 11.

CLITHROCYTHERIDEA JESSUPENSIS (Howe & Garrett), 1934
Plate 2, figures 20–22

Cytheridea ? jessupensis HOWE & GARRETT, 1934, Louisiana Dept. Cons., Geol. Bull. 4, pp. 32–33, pl. 1, figs. 19–21.

Dimensions of figured specimens.—Double valve, length .53 mm., width .28 mm. Right valve, length .54 mm., height .27 mm. Left valve, length .56 mm., height .30 mm.

Hypotype.—AMNH (right valve) OT-133; (left valve) OT-134; (double valve) OT-135.

Occurrence.—Abundant in the Coal Bluff. According to Howe, it is rare in the lower Wilcox of Louisiana.

Remarks.—The Coal Bluff specimens differ from the type in the manner of overlap; that of the type extends around the entire periphery, whereas the Coal Bluff specimens lack the overlap at the middle of the hinge line.

CLITHROCYTHERIDEA ALEXANDERI Stephenson, 1938
Plate 2, figures 10–13

Cytheridea (*Clithrocytheridea*) *alexanderi* STE-

PHENSON, 1938, Jour. Paleontology, vol. 12, pp. 575–576, pl. 67, figs. 19, 20; text figs. 33, 34.

Dimensions of figured specimens.—Adults, right valve, length .79 mm., height .36 mm. Left valve, length .77 mm., height .42 mm. Young, right valve, length .35 mm., height .19 mm., left valve, length .34 mm., height .20 mm.

Hypotype.—AMNH (right valve) OT-136; (left valve) OT-137.

Occurrence.—Abundant in the Coal Bluff. Stephenson describes it as being common in the Naheola formation at Matthews Landing, Wilcox County, Alabama, and as rare in the Naheola formation at Naheola Landing, Choctaw County, Alabama.

Remarks.—The ornamentation of the Caledonia specimens seems to exhibit more parallel alignment to the free margins than in those figured by Alexander.

CLITHROCYTHERIDEA RUIDA (Alexander), 1934
Plate 2, figures 14–18

Cytheridea ruida ALEXANDER, 1934, Jour. Paleontology, vol. 8, p. 224, pl. 33, fig. 7.

Remarks.—The males are more elongate than the females, with a more concave ventral margin and a more pointed posterior. In the female the prominent dorsal ridge is slightly shorter and higher. The young are proportionally narrower at the posterior than the adults. The surface ornamentation holds true through all molt stages.

Dimensions of figured specimens.—Double valve, length .62 mm., width .31 mm. Right valve, length .62 mm., height .32 mm. Left valve, length .66 mm., height .40 mm. Young, right valve, length .34 mm., height .19 mm. Left valve, length .35 mm., height .21 mm.

Hypotype.—AMNH (double valve) OT-138.

Occurrence.—Rather common in the Coal Bluff at Caledonia. Alexander found it in some exposures of the Kincaid formation of Texas.

CLITHROCYTHERIDEA MACROLACCUS Munsey, n. sp.
Plate 3, figures 1–3

Description.—Carapace elongate, subtriangular, highest in front of center. Dorsal margin arched, nearly straight along hinge line; anterior broadly and obliquely rounded; ventral margin straight to slightly sinuate; posterior end subacutely rounded. Anterior rim usually bears six to ten rather prominent teeth, but these may vary in size and number; two prominent elongate teeth extend from the posterior end, the lower one being much longer than the upper. Entire surface covered by rounded, deep reticulations, those near the center forming four or five low, rounded vertical ridges. On the interior of the valves these ridges conform to a depressed area. A prominent ridge is located a short distance from, and parallel to, the anterior margin. In dorsal view the carapace is convex, being slightly flattened and widest at the middle, and with subacute ends. Internal features typical of genus.

Dimensions of figured specimens.—Adults, right valve, length .65 mm., height .34 mm. Left valve, length .65 mm., height .39 mm. Young, right valve, length .50 mm., height .29 mm.

Holotype.—AMNH (left valve) OT-139; paratype (right valve) OT-140.

Occurrence.—Common in the Coal Bluff.

Genus EUCYTHERE Brady, 1866

Eucythere BRADY, 1866, Linnean Soc. London, Trans., vol. 26, p. 429.
Eucythere ALEXANDER, 1934, Jour. Paleontology, vol. 8, p. 226.
Eucythere ALEXANDER, 1936, Jour. Paleontology, vol. 10, p. 689.
Eucythere TRIEBEL, 1940, Senck., vol. 22, pp. 161–162.
Eucythere BONNEMA, 1940, Nat. Maand., 29e, No. 11, p. 116.

Type species: *Cythere declivis* Norman, 1865, Nat. Hist. Trans. Northumb. and Durham., vol. 1, p. 16, pl. 5, figs. 9–12. Syn. *Cytheropsis* Sars, 1865 (non *Cytheropsis* M'Coy, 1855).

EUCYTHERE TRIORDINIS Schmidt, 1948
Plate 3, figure 6

Eucythere triordinis SCHMIDT, 1948, Jour. Paleontology, vol. 22, p. 411, pl. 63, figs. 26, 27.

Dimensions of figured specimen.—Length .59 mm., height .32 mm.

Hypotype.—AMNH (right valve) OT-141.

Occurrence.—Very rare in the Coal Bluff of Alabama. According to Schmidt, rare in the Aquia formation of Virginia and Maryland.

Subfamily LOXOCONCHINAE Sars, 1926
Genus LOXOCONCHA Sars, 1865

Loxoconcha SARS, 1865, Oversigt Norges Marine Ost., p. 61.
Loxoconcha SARS, 1926, Account Crustacea Norway, vol. 9, pp. 217–222.
Loxoconcha ALEXANDER, 1936, Jour. Paleontology, vol. 10, p. 693.
Loxoconcha MURRAY, 1938, Jour. Paleontology, vol. 12, pp. 586–587.
Loxoconcha EDWARDS, 1944, Jour. Paleontology, vol. 18, pp. 526–527.

Type species: *Cythere rhomboidea* Fischer, 1855 = *Cythere impressa* Baird, 1850 (non M'Coy) = *Loxoconcha bairdi* Müller, 1894.

LOXOCONCHA CORRUGATA Alexander, 1934
Plate 1, figures 7–8

Loxoconcha corrugata ALEXANDER, 1934, Jour. Paleontology, vol. 8, p. 228, pl. 33, fig. 13.
Loxoconcha corrugata HARRIS & JOBE, 1951 Microfauna Midway Ark., p. 73, pl. 14, fig. 3'.

Dimensions of figured specimens.—Right valve, length .32 mm., height .21 mm. Left valve, length .30 mm., height .19 mm.

Hypotype.—AMNH (right valve) OT-142; (left valve) OT-143.

Occurrence.—Rare in the Coal Bluff. Very rare in the Wills Point and Kincaid formations of Texas.

LOXOCONCHA NOTOAULAX Munsey, n. sp.
Plate 3, figures 9–10

Description.—Carapace subrectangular, elongate. Dorsal margin straight to gently concave; anterior obliquely rounded with a narrow, compressed border; ventral margin straight, curving gradually upward posteriorly to form a short, blunt caudal process. Shell depressed just anterior to middle. Thickest near posterior. Elongate tubercle just below anterodorsal margin. Surface strongly reticulate with well-defined pits and low, rounded ridges somewhat aligned with the borders of the carapace. A rather distinct marginal ridge begins at the postventral angle where it is marked by a prominent depression just above its dorsal edge. It extends the length of, and subparallels, the ventral margin, swings upward parallel to the anterior edge. A less distinct, irregular middle ridge begins near the posterior and extends approximately two-thirds the length of the carapace. Another ill-defined ridge runs the length of the dorsal margin. Internal features typical of genus.

Dimensions of figured specimens.—Left valve, length .35 mm., height .21 mm. Right valve, length .38 mm., height .19 mm.

Holotype.—AMNH (left valve) OT-144; paratype (right valve) OT-145.

Remarks.—This species differs from *Loxoconcha mcbeanensis* Murray in that the prominent ventral ridge does not converge with the marginal ridge.

Genus CYTHEROPTERON Sars, 1865
Subgenus CYTHEROPTERON Sars, s. s.

Cytheropteron SARS, 1865, Oversigt Norges Marine Ost., pp. 79–80.
Cytheropteron SARS, 1926, Account Crustacea Norway, vol. 9, p. 232.
Cytheropteron (*Cytheropteron*) ALEXANDER, 1933, Jour. Paleontology, vol. 7, p. 181.
Cytheropteron MARTIN, 1939, Jour. Paleontology, vol. 13, pp. 176–182.
Cytheropteron STEPHENSON, 1946, Jour. Paleontology, vol. 20, p. 318.

Type species: *Cythere latissima* Norman, 1865, Nat. Hist. Trans. Northumb. and Durham, vol. 1, p. 19, pl. 6, figs. 5–8. Syn. *Cytheropteron convexum* Sars, 1865.

CYTHEROPTERON (CYTHEROPTERON) HINCHEYI Munsey, n. sp.
Plate 2, figures 3–7

Description.—Carapace small, ovate. Dorsal margin straight to very gently arched; anterior obliquely rounded; ventral margin gently convex, obscured by alate projection; middle of posterior carries a blunt, upturned caudal process in the young which becomes more horizontally disposed in the adult. A low, very indistinct marginal ridge circumscribes the periphery of the valves. A strongly developed ventral wing shows an inflated edge. Faint, wide median sulcus or groove present. Surface covered with small reticulations and numerous, low, rounded ridges generally aligned with the short axis of the carapace. A number of these ridges begin at the posterior half of the dorsal marginal rim and extend ventrally in an irregular manner to the thickened edge of the ala. Anterior half of the carapace is ornamented with similar ridges which curve around the border of the wide, flat sulcus.

Internal features typical for the genus. There may be a reversal of the usual expression of dimorphism in this species. The elongate, narrow specimens carry a much more bulbous posterior than the shorter ones, which suggests that the females may be the more elongate form. The reticulations

and ridges are more evident in the young, the ridges almost disappearing in the adult. The young carapace is much thinner and less rounded with a more blunted caudal process than that possessed by the adult. The vertical pattern of muscle scars is usually quite evident even on the exterior of the carapace.

Dimensions of figured specimens.—Left valve, rounded form, length .53 mm., height .34 mm. Left valve, elongate form, length .53 mm., height .30 mm. Right valve, rounded form, length .52 mm., height .30 mm. Smallest molt, right valve, length .45 mm., height .25 mm.

Holotype.—AMNH (right valve) OT-146; paratype (left valve) OT-147.

Occurrence.—Rather rare in the Coal Bluff.

Remarks.—This species is named in honor of Dr. Norman S. Hinchey of Washington University, St. Louis, Missouri.

CYTHEROPTERON (CYTHEROPTERON) LIOGLUMA Munsey, n. sp.
Plate 3, figure 22

Description.—Carapace small, elongate, ovate. Dorsal margin arched with a central flattening; anterior obliquely rounded; ventral margin nearly straight, largely obscured by the curved alate process; posterior narrowly rounded with a dorsal flatness; no posterior caudal process present. Greatest height and width just posterior to middle. Carapace strongly convex in end view with a moderately developed alate process extending the length of the shell. Surface evenly covered with large, shallow, irregularly shaped and arranged reticulations. Internal features typical for genus.

Dimensions of figured specimen.—Length .34 mm., height .19 mm.

Holotype.—AMNH (right valve) OT-148.

Occurrence.—Very rare in the Coal Bluff.

Remarks.—This species resembles *C. subreticulatum* Van den Bold, but differs in the lack of the posterior division of the alate ridge. It lacks the sharp alate ridge and caudal process of *C. variosum* Martin.

Subfamily BYTHOCYTHERINAE Sars, 1926
Genus MONOCERATINA Roth, 1928

Monoceratina ROTH, 1928, Jour. Paleontology, vol. 2, p. 15.
Monoceratina ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 57–60.
Monoceratina ALEXANDER, 1934, Jour. Paleontology, vol. 8, pp. 230–231.
Monoceratina TRIEBEL & BARTENSTEIN, 1938, Senck., vol. 20, pp. 502–518.
Monoceratina TRIEBEL, 1941, Senck., vol. 23, pp. 318–319.
Monoceratina STEPHENSON, 1946, Jour. Paleontology, vol. 20, pp. 312–313.

Type species; *Monoceratina ventrale* Roth. 1928, Jour. Paleontology, vol. 2, p. 16, figs. 1a–1c.

MONOCERATINA BIPHYSA Munsey, n. sp.
Plate 3, figure 23

Description.—Carapace small, subrhomboidal. Dorsal margin long and straight; anterior obliquely truncated; ventral margin curves upward to a rather elongate, subrounded postdorsal caudal process. The carapace is divided into two approximately equal halves by a sulcus. The posterior half is marked by a very prominent, ovate node, and the anterior by a lower, rounded node. A wing-like process, with a somewhat thickened edge, extends almost the full length of the ventral margin. A low, rounded ridge, parallel to and a short distance from the anterior margin, extends around the dorsal margin and curves downward just before reaching the postdorsal angle. It terminates under the ventral edge of the caudal process. Surface covered by very shallow, indistinct reticulations. Muscle scar pattern obscured. A left valve, the only specimen found, shows the hinge to consist of a narrow crenulate bar.

Dimensions of figured specimen.—Length .37 mm., height .22 mm.

Holotype.—AMNH (left valve) OT-149.

Occurrence.—Very rare.

Subfamily CYTHERURINAE Müller, 1894
Genus CYTHERURA Sars, 1865

Cytherura SARS, 1865, Oversigt Norges Marine Ost., p. 69.
Cytherura ALEXANDER, 1936, Jour. Paleontology, vol. 10, pp. 690–691.
Cytherura STEPHENSON, 1946, Jour. Paleontology, vol. 20, pp. 316–317.

Type species: *Cythere gibba* Müller, 1785, Entomostraca, p. 66, pl. 7, figs. 7–9.

CYTHERURA DORILAEMUS Munsey, n. sp.
Plate 3, figure 7

Description.—Carapace subrectangular to ovate. Dorsal margin straight; anterior obliquely rounded with a somewhat compressed border; ventral margin gently concave, in end view appears flattened; poste-

rior caudal process elongate, rounded, situated slightly below the center of the carapace. Thickest near posterior, where a globular swelling occurs. A very obscure, shallow, dorsal sulcus divides the carapace into two approximately equal parts. Surface covered by elongate, shallow reticulations more or less crudely aligned with the long axis of the carapace, forming low, rounded, indistinct irregularly arranged ridges. A more or less prominent ridge originates at the postventral angle, extends upward and anteriorly, branches into three low, obscure ridges which terminate at the anterior marginal rim; between these ridges on the anterior there are four shallow, broad depressions. Internal features typical of genus.

Dimensions of figured specimen.—Length .38 mm., height .18 mm.

Holotype.—AMNH (right valve) OT-150.

Occurrence.—Rare.

CYTHERURA OXYCRURIS Munsey, n. sp.
Plate 1, figures 22–23

Description.—Carapace ovate to subrectangular. Dorsal margin straight to very gently convex. Anterior obliquely rounded; ventral margin sinuate; posterior caudal process elongate, narrow, situated slightly above the middle. A well-defined sulcus is anterior to the center. Circumscribing the entire periphery of the carapace is a very narrow, low marginal rim. A very pronounced ventral alate process includes the posterior two-thirds of the carapace. The rim of the ala is thickened by a ridge which bifurcates at the posterior extremity, the upper element splits into three ridges extending to the anterior marginal ridge and divides the anterodorsal area into two approximately equal, wide, shallow depressions. The lower segment extends to the lower part of the anterior margin, forming two well-defined depressions. An indistinct ridge originates at the base of the caudal process and extends anteriorly for a short distance. Internal features typical for genus.

Dimensions of figured specimens.—Right valve, length .37 mm., height .21 mm. Left valve, length .38 mm., height .19 mm.

Holotype.—AMNH (right valve) OT-151.

Occurrence.—Very rare.

Remarks.—This species differs from *C. dorilaemus* in the type and arrangement of the ornamentation, and in having a more pronounced alate structure.

CYTHERURA PHASEOUS Munsey, n. sp.
Plate 3, figure 8

Description.—Carapace elongate, subrectangular. Dorsal margin straight; anterior obliquely rounded; ventral margin straight to very gently concave; posterior caudal process short and blunt, located a little above the center of the carapace. A wide, very shallow dorsal sulcus is situated slightly anterior to the middle. Posterior somewhat bulbous. The surface is covered with shallow reticulations, roughly aligned and forming indistinct, nearly horizontal ridges. Some specimens show a narrow keel beginning at the anterior, extending along the venter, and terminating beneath the posterior caudal process. Internal features typical for genus. Male differs from female in being more elongate and possessing a less pronounced caudal process.

Dimensions of figured specimen.—Length .35 mm., height .16 mm.

Holotype.—AMNH (left valve) OT-152; paratype (double valve) OT-153.

Occurrence.—Rare.

CYTHERURA BOLDI Munsey, n. sp.
Plate 2, figure 19

Description.—Carapace tear-shaped, somewhat variable in outline. Dorsal margin straight to convex; anterior narrowly to broadly rounded; ventral margin convex to sinuate, curving upward into a very short, blunt caudal process at the middle of the posterior. Venter flattened in end view. Surface covered by numerous, low, rounded longitudinal ridges, those on the ventral portion curving upward at the posterior and anterior ends of the carapace; those of the dorsal curving downward, the two converging slightly below the middle at the anterior and posterior margins. The grooves between the ridges contain numerous shallow pits. Internal features those of genus.

Dimensions of figured specimen.—Length .35 mm., height .19 mm.

Holotype.—AMNH (left valve) OT-154; paratype (right valve) OT-155.

Occurrence.—Relatively common in the Coal Bluff.

Remarks.—This species differs from *C. taylorensis* Alexander in the arrangement of the ridges and nature of the caudal process. Named in honor of Dr. W. A. Van den Bold.

Genus EUCYTHERURA Müller, 1894

Eucytherura MÜLLER, 1894, Fauna Flora Golfes Neapel, Mon. 21, Ostracoden, p. 305.
Eucytherura ALEXANDER, 1936, Jour. Paleontology, vol. 10, p. 692.
Eucytherura WEINGEIST, 1949, Jour. Paleontology, vol. 23, pp. 364–371.

Type species: *Cythere complexa* Brady, 1867, Rept. British Assoc. Adv. Sci., p. 210.

EUCYTHERURA LATEBROSA Weingeist, 1949
Plate 2, figures 8–9

Eucytherura latebrosa WEINGEIST, 1949, Jour. Paleontology, vol. 23, p. 375, pl. 73, figs. 14, 17.

Dimensions of figured specimens.—Right valve, length .28 mm., height .17 mm. Left valve, length .29 mm., height .18 mm.

Hypotype.—AMNH (left valve) OT-156; (right valve) OT-157.

Occurrence.—Common in the Coal Bluff.

Subfamily XESTOLEBERINAE Sars, 1928
Genus MICROXESTOLEBERIS Müller, 1894

Microxestoleberis MÜLLER, 1894, Fauna Flora Golfes Neapel, p. 339.

Type species: *Microxestoleberis nana* Müller, 1894, Fauna Flora Golfes Neapel, pp. 339–340, pl. 39, figs. 1, 6, 7, 40–48.

Description.—Carapace in side view small, elongate, fragile. Greatest height near the middle, thickest posterior to middle. Dorsal margin gently to flatly arched; anterior margin unevenly rounded, bluntly rounded at anteroventral angle; ventral margin nearly straight, obscured by development of lower portion of carapace; posterior tending to be bluntly pointed, curving sharply into postdorsal angle. In end view, venter greatly flattened. Hinge apparently without teeth, left valve overlapping the right. No surface ornamentation. Scar pattern consists of a nearly vertical row of four scars, anterior to which is a U-shaped scar. Dorsal to this and close to the dorsal margin is an elongate, gently arched scar. Normal pore canals comparatively large, few, evenly scattered. Radial pore canals few, irregular. Inner margin and line of concrescence do not coincide. Inner margin broadest at, and parallel to, anterior, wide at postventral angle. Line of concrescence broadest at anterior and postdorsal angle.

MICROXESTOLEBERIS WESTMORELANDI
Munsey, n. sp.
Plate 1, figures 14, 15

Description.—Carapace minute, fragile, subovate, thickest slightly posterior to middle. Dorsal margin rather strongly arched, highest just anterior to middle, sloping toward each end with the anterior slope more pronounced than that of the posterior. Anterior margin acutely rounded; ventral margin straight, sloping upward slightly at each end; posterior narrowly rounded, forming almost a right angle with the venter. Venter flattened in end view. Surface smooth. Minute size and rather poor preservation prevent a detailed hinge description. Other internal features typical of genus.

Dimensions of figured specimens.—Left valve, length .34 mm., height .16 mm. Right valve, length .39 mm., height .16 mm.

Holotype.—AMNH (left valve) OT-158; paratype (right valve) OT-159.

Occurrence.—Very rare in the Coal Bluff.

Remarks.—Named in honor of F. S. Westmoreland, senior paleontologist, Atlantic Refining Co., Houston, Texas.

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THE INSECTIVORES OF THE REXROAD FAUNA, UPPER PLIOCENE OF KANSAS

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ABSTRACT—Six genera of insectivores were recovered with associated vertebrates from a deposit of the upper Pliocene, Rexroad formation, Meade County, Kansas. The insectivores are *Hesperoscalops*, a mole, which is probably ancestral to the recent genus *Scalopus;* the following genera of shrews: *Sorex*, *Paracryptotis*, *Cryptotis?*, *Blarina* and *Notiosorex*. Three species are described as new. The upper Pliocene distribution of the shrews in North America was different than at the present. This difference is accounted for by the climatic change which has occurred in the region where the fossils were recovered.

During the past five years considerable data has been accumulated upon the rather poorly known insectivores from the upper Pliocene, Rexroad fauna of southwestern Kansas. The distribution of the genera of shrews in the upper Pliocene is an entirely different picture than that at the present time. Much of this difference in distribution is due to climatic change in the area and to the shifting of the ranges of forms during the Pleistocene. The specimens herein reported were all taken from a small exposure of the Rexroad formation in Fox Canyon, Meade County, Kansas, unless otherwise stated. A discussion of the associated mammalian fauna and of the Rexroad formation is given by Hibbard (1950). Only one species of mole is known in the Rexroad fauna. Five genera and five species of shrews were recovered from an area less than fifteen feet long, within a vertical range of two feet, and extending back into the exposure approximately three feet. At the present time only one species of mole, *Scalopus aquaticus intermedius* (Elliot), and one shrew, *Cryptotis parva* (Say) are known to live in that part of the High Plains.

I am particularly indebted to the University of Michigan Museum field parties of the summers of 1950 and 1951; and to the Kansas Forestry, Fish and Game Commission for living quarters and for permission to use stream facilities for the recovery of the fossil vertebrates. Mr. J. D. Center, of the Triangle T Ranch, Plains, Kansas, who has leased the land of the late Alexander W. Adams, kindly gave us permission to continue the collection of fossils and the study of deposits on this land. This study was started in the summer of 1936, with the permission and cooperation of Alex(ander) W. Adams of Maple Hill, Kansas.

This work was aided by the loan of specimens under the care of Dr. W. H. Burt, University of Michigan; Mr. Stanley P. Young and Miss Viola S. Schantz, United States Fish and Wildlife Service; and Dr. Robert W. Wilson, University of Kansas, who also gave permission to figure the specimen of *Sorex taylori* and who checked certain characters on specimens in the collections at the University of Kansas. The line drawings were made by W. C. Sherman and Jane S. Mengel. All specimens are in the University of Michigan Museum collection unless otherwise stated. The illustrations of this paper were made possible by the financial support accorded to the writer by the Faculty Research Fund of the University of Michigan.

Order INSECTIVORA
Family TALPIDAE
HESPEROSCALOPS REXROADI Hibbard
Figure 1A–D

Hesperoscalops rexroadi HIBBARD, 1941, Amer. Midl. Nat., vol. 26, pp. 337–339, fig. 1.

The remains of this mole are not common in the deposits containing the Rexroad fauna. Fragmentary remains have been taken that furnish considerable information regarding the form.

Five humeri, part of an ulna, a complete ulna, the distal end of a scapula, parts of

three right and three left rami, part of a right maxillary, and isolated teeth were recovered in the summers of 1950 and 1951 from the deposit in Fox Canyon, on the XI Ranch, Meade County, Kansas.

No complete upper or lower dentitions were found. The most perfect specimen recovered was a right ramus, no. 28141, containing M_1–M_3 and the alveoli of the other teeth. The lower dentitional formula is, two incisors, no canine, three premolars and three molars. The teeth of this specimen are worn down to the basal accessory cusps (fig. 1D) which project horizontally to the crown from the side of the tooth. Cement is present in the external valley and on the anterior face of each tooth but not present on the internal surface. The high-crowned teeth are closely set and the crowns of the teeth are separated only by the basal accessory cusps (see fig. 1B). The anteroposterior alveolar length of M_1–M_3 of three specimens is 7.8, 7.15 and 7.6 mm. The only lower premolar recovered was P_4 in specimen no. 27279 (fig. 1C). Three of the rami, nos. 27279, 28141 and 28142 are complete enough to show the mental foramina. The foramina are two in number. The posterior mental foramen is located below the alveolar border between P_4 and M_1. The anterior mental foramen is nearly twice as large as the posterior and is located below the midline of P_3.

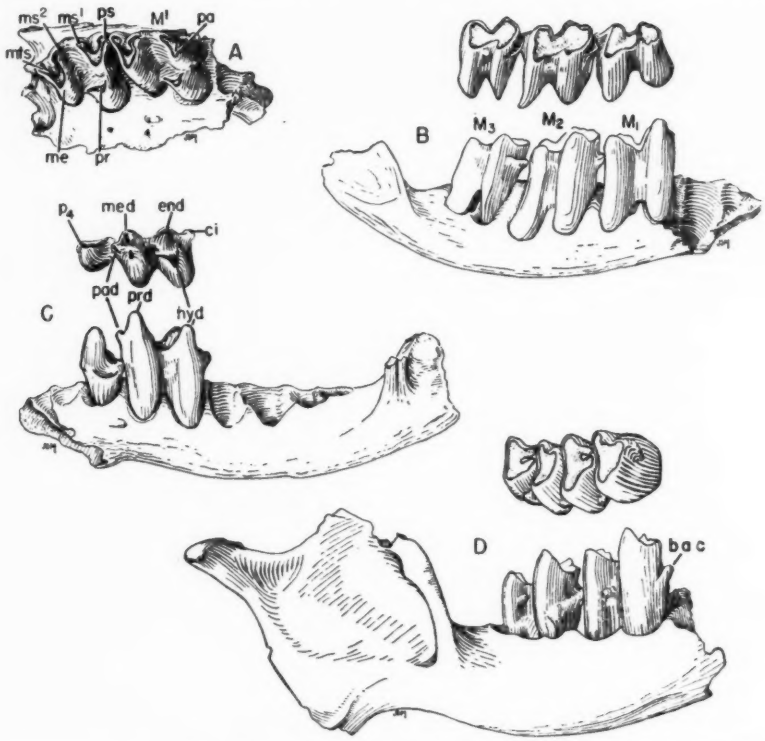


FIG. 1—*Hesperoscalops rexroadi* Hibbard, from Rexroad formation, Meade County, Kansas. *A*, right maxillary, no. 27277 with M^1–M^2 occlusal view. *B*, right ramus, no. 27278, with M_1–M_3. *C*, left ramus, no. 27279, with P_4–M_1. *D*, right ramus, no. 27276, with M_2–M_3. Lateral and occlusal views. All ×4. Abbreviations: bac., basal accessory cusps; ci., cingulum; end., entoconid; hyd., hypoconid; me., metacone; med., metaconid; ms^1., mesostyle-one; ms^2., mesostyle-two; pa., paracone; pad., paraconid; pr., protocone; prd., protoconid; ps., parastyle.

The fragmentary right maxillary, no. 27277, contains M^1 and M^2, and parts of the alveoli of P^4 and M^3 (fig. 1A). The anteroposterior length of M^1–M^2 is 5.8 mm. The crowns of M^1 and M^2 fit closely together

along the labial side. P^4 rested against M^1 and so did M^3 against M^2. The closeness of the teeth is in contrast to the widely spaced teeth in the genus *Scalopus*. In *Hesperoscalops* wide and deep valleys separate the parastyle and mesostyle-one, also mesostyle-two and the metastyle. The notch between the maxillary and the jugal process of the maxillary ends just opposite the posterior edge of M^2. The notch is situated as in *Scalopus*. In *Scapanus* the notch ends at the midline of M^3.

The humeri, ulnae, and distal part of the scapula are not as large or as heavily developed as these elements in *Scalopus*.

Part of an associated individual, no. 27276, consisting of the anterior part of the left ramus with M_1, the posterior part of the right ramus with M_2–M_3 (fig. 4D), an ulna, the distal part of a scapula, and the proximal head of a femur was collected in the summer of 1950 in the NE ¼ sec. 35, T. 34 S., R. 31 W., Seward County, Kansas. The specimen was taken from silty clay just below the sandy silt containing *Testudo riggsi* Hibbard (1944), approximately 60 yards east of the type locality of the turtle. The teeth are near the same stage of wear as in the holotype specimen of *H. rexroadi*. The specimen is slightly larger but the cusp pattern of the teeth is the same. The anteroposterior diameter of M_2–M_3 including the basal accessory cusps is 5.7 mm.

Hibbard (1941a and 1950) reported the presence of the Recent genus *Scalopus* as a part of the Rexroad fauna based upon a humerus taken at Locality no. 2, Meade County, Kansas. A study of the remains of the mole recovered from the upper Pliocene deposits of Kansas shows that only one genus, *Hesperoscalops*, has been taken in association with the other vertebrates. From a study of the material at hand it is evident that *Hesperoscalops* is closely related to *Scalopus*. *Hesperoscalops* is probably the ancestral stock from which *Scalopus* was developed. Both *Hesperoscalops* and *Scalopus* possess high-crowned teeth. The distinctive difference between the two genera is the lack of, or the greatly reduced basal accessory cusps in *Scalopus*. Also the widely spaced teeth of *Scalopus* are in contrast to the teeth of *Hesperoscalops* which fit closely together.

Family SORICIDAE

SOREX REXROADENSIS Hibbard, n. sp.

Figures 2D, 3E

Holotype.—No. 28147, University of Michigan Museum of Paleontology; posterior part of left ramus, with M_1–M_3. Metaconid broken on M_1. Collected by Claude W. Hibbard and party, summer of 1951.

Type locality.—University of Michigan locality, UM-Kl-47, in Fox Canyon, sec. 35, T. 34 S., R. 30 W., XI Ranch, Meade County, Kansas.

Age.—Upper Pliocene, Rexroad formation, Rexroad fauna.

Diagnosis.—A small shrew the size of *Sorex preblei* Jackson with a slightly heavier ramus. Talonid of M_1 and M_2 not as wide in comparison to the trigonid as in recent species of *Sorex*. The entoconid more distinctly separated from the metaconid in M_1 and M_2 than in recent forms of *Sorex*. Tip of protoconid on both teeth projects lingually past the longitudinal axis of M_1 and M_2.

Description of holotype.—Shape of articular condyle as in *Sorex preblei* with the lower articular surface slightly larger than in *S. preblei*. The *posterointernal ramal fossa*,[1] fig. 5B (pterygoid fossa, muscular fossa, internal temporal fossa, etc. of authors), extending farther upward on the ascending ramus than in *Sorex preblei*. In *Sorex preblei* a distinct ridge separates the top of the posterointernal ramal fossa from a slight depression above the ridge. In *Sorex rexroadensis* no bony ridge is present and the depression occurs at the upper edge of the fossa, which produces a fossa with a greater height.

External and internal cingulum of M_1–M_3 broader than in *Sorex preblei* and *S. nanus* Merriam. Mental foramen situated below posterior border of protoconid of M_1. Anteroposterior length of M_1–M_3 is 2.91 mm.

Discussion.—*Sorex rexroadensis* is the smallest known Pliocene shrew of North America. It is impossible to assign it to any living group of *Sorex*. This shrew appears to have been rare in the Rexroad fauna. It may

[1] So far as is known the term *posterointernal ramal fossa* is used for the first time. The term was proposed by Doctor Hartley H. T. Jackson because of the confusion of the terms pterygoid and temporal fossae which apply to fossae on the cranium.

have been an upland form in contrast to *Sorex taylori* which is considered as a moist lowland dweller.

SOREX TAYLORI[2] Hibbard
Figure 2A

Sorex taylori HIBBARD, 1938, Trans. Kansas Acad. Sci., vol. 40, pp. 242–243, fig. 1.

This shrew has only been recovered from localities no. 2 and 3 in the Rexroad formation in Meade County, Kansas. Lower jaws of this shrew are common in the deposit at locality no. 3. For a discussion of these localities see Hibbard, 1950, pp. 168 and 173. Hibbard, 1941b and 1950, considered the deposits at locality no. 3 as having been laid down in ponded water, either in an oxbow lake or back of a beaver dam.

The heavy rains during the spring of 1951, eroded away much of the present stream bank at locality no. 3, which is developed in the Rexroad formation. The erosion exposed two fine sand pockets about eighteen inches in diameter in the silt and clay below the lignite seams on a level with the present bed of the stream. These pockets of fine white sand fingered upward a short distance into the overlying silt and clay. The sand pockets extended downward in a sand tube. Due to weather conditions it was impossible to follow the tubes downward or to completely excavate the immediate area surrounding the pockets. Nearly fifty pounds of the fine sand from one of the pockets was removed. It consisted of a mass of broken and polished bone. This sand was dried and washed. Approximately two gallons of teeth, scraps of turtle, abundant fragments of large limb bones and jaws of small mammals were recovered, including parts of four lower jaws of *Sorex taylori*. It now appears that the basin in which these deposits were laid down at locality no. 3 was developed by a large artesian spring.

It appears that the present stream has only removed, in part, the very top of the old artesian system. In an old basin developed by an artesian spring the upward flow of the water becomes dendritic in pattern. As sediments accumulate in the basin along with the heavy growth of vegetation which chokes the small outlets of the spring, more water issues from other openings which become enlarged and new outlets are developed in areas free of overburden. There is then a subsurface shifting of the dendritic pattern which increases the size of the basin. The location of the outlets of the artesian spring is marked by upward boiling of water through openings in the substrata which are filled with fine sand. This sand is set in motion by the escaping water which gives a boiling or churning effect to the sand. This condition can be observed at many of the present artesian springs along Crooked Creek Valley, near Meade, Kansas.

Upper Pliocene artesian spring deposits and a Pleistocene artesian spring deposit in this region containing vertebrate fossils were described by Hibbard and Riggs (1949, pp. 830–831).

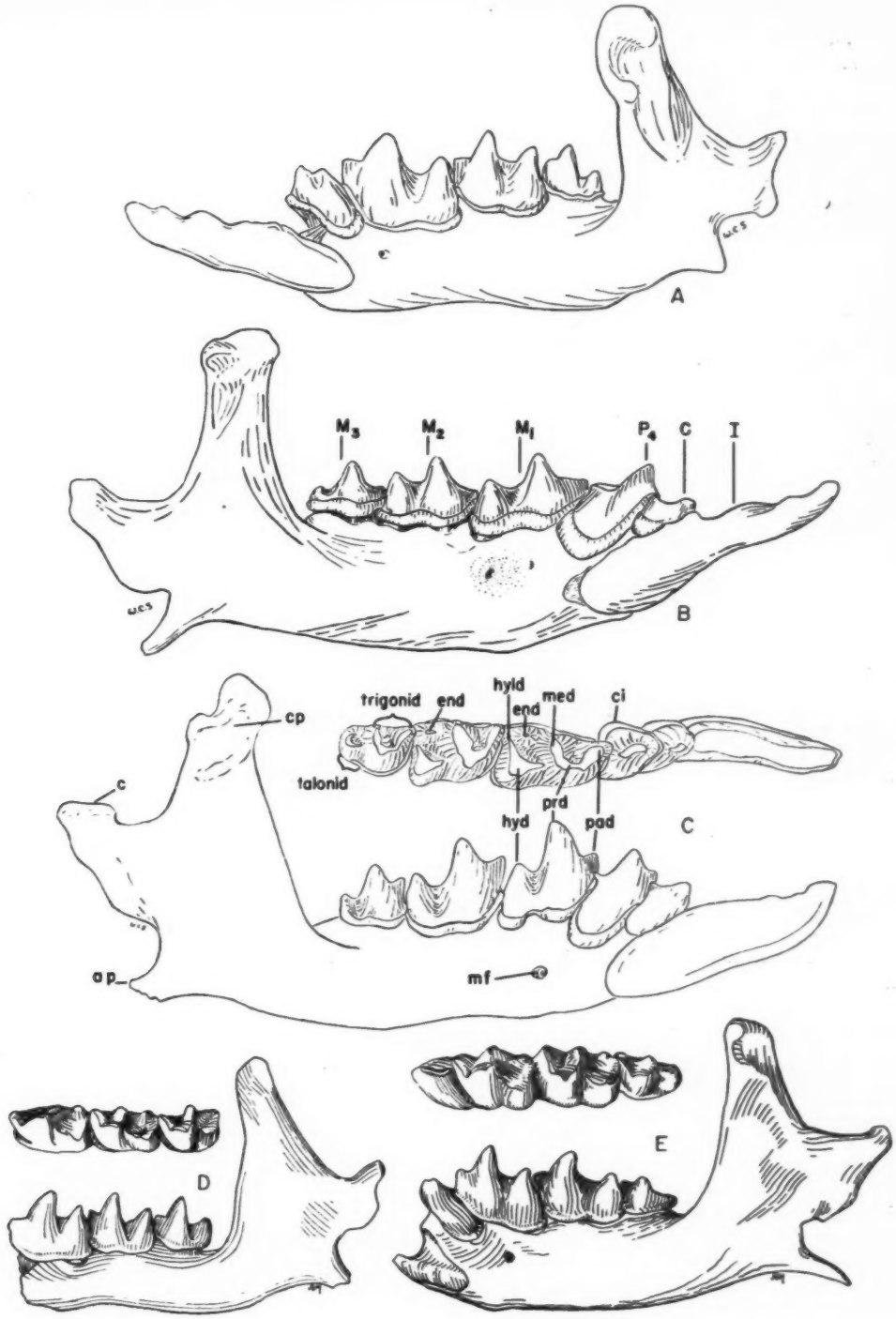
PARACRYPTOTIS REX Hibbard
Figures 3A, 3F, 4E

Paracryptotis rex HIBBARD, 1950, Contrib. Mus. Paleontol. Univ. Michigan, vol. 8, no. 6, pp. 122–127, figs. 2 and 3.

Parts of 21 individuals of this large shrew have been taken from the Fox Canyon deposit in association with the rest of the fauna. This count is based on the number of right lower jaws recovered.

[2] This species was named for Doctor Edward H. Taylor, University of Kansas, who offered many helpful criticisms and suggestions in the study of the fauna. Due to a *lapsus calami* this did not appear with the original description.

FIG. 2—*A*, *Sorex taylori* Hibbard, lateral view of left ramus, Kansas University no. 4615. *B*, *Blarina adamsi* Hibbard, n. sp., lateral view of right ramus, U.M.M.P. no. 24352. *C*, *Notiosorex jacksoni* Hibbard, lateral and occlusal views of right ramus, U.M.M.P., no. 24354. *D*, *Sorex rexroadensis* Hibbard, n. sp., holotype, lateral and occlusal views of part of left ramus, U.M.M.P. no. 28147. *E*, *Cryptotis? meadensis* Hibbard, n. sp., holotype, lateral and occlusal views of left ramus, U.M.M.P., no. 27266. All ×10. Abbreviations: ap., angular process; c., condyle; ci., cingulum; cp., coronoid process; end., entoconid; hyd., hypoconid; hyld., hypoconulid; med., metaconid; mf., mental foramen; pad., paraconid; prd., protoconid.


A
M_3
M_2
M_1
P_4
C
I
B
trigonid
end
hyld
end
med
ci
talonid
cp
c
hyd
prd
pad
C
ap
mf
D
E

In the holotype there is a small space on the labial side of the maxillary between the canine and P^4 through which the labial side of the reduced P^3 may be seen. In specimen no. 27209 (fig. 4E) the right canine rests against the anterior edge of RP^4 on the labial side. The space which is present on the left side of the maxillary between the canine and P^4 appears to be due in part to the loss of I^3 which has allowed the canine to shift forward. The above specimen is that of an old adult. The teeth are considerably worn. The distance between the lingual edges of the right and left P^3, the fourth unicuspids, is 2.1 mm. The maximum length of M^1–M^3 is 4.3 mm. and 3.9 mm. in the holotype. Specimen no. 28375 consists of a nearly complete palate lacking part of the right maxillary. The dentition of this specimen is intermediate in wear between the holotype no. 25172, and specimen no. 27209. The greatest anteroposterior length of I^1–M^3, no. 28375, is 11.65 mm. All of the teeth show pigmentation on the crowns except P^3 and M^3, which are white. Specimen no. 28376 consists of the palatal region of a young adult, bearing LI^3, C, and P^4–M^3; and RC–M^3. The cusps of the teeth are unworn. The specimen is light brown in color. Pigmentation can not be observed in the crowns of the teeth.

The lower jaws vary in color from white to dark brown. The white specimens and light-colored specimens show pigmentation on the crowns of all of the lower teeth. The elongated incisor has a large median lobe (fig. 3F). Specimen no. 28386 is part of the right ramus of a young individual. The unworn talonid of M_3 has a well-developed basin. The range of measurements of 20 lower dentitions of all ages are as follows: greatest anteroposterior length of M_1–M_3 is 4.8 mm. to 5.7 mm., average 5.26 mm. Of eight specimens the greatest anteroposterior length of C–M_3 is 6.4 mm. to 7.2 mm; average 6.86 mm. The shape of the condyle with its two articular surfaces is distinct from the other shrews with which it was associated

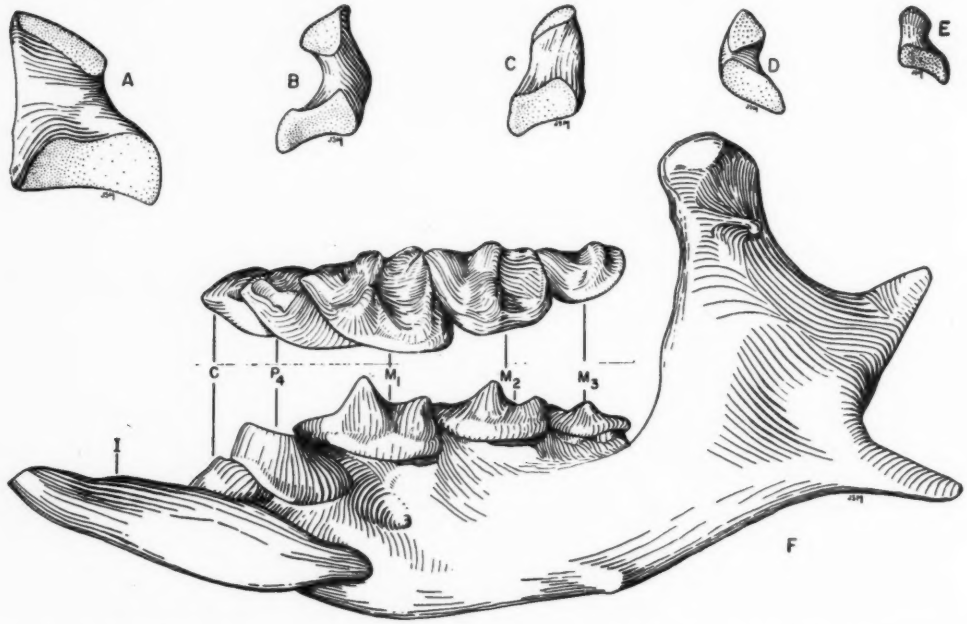


FIG. 3—*A–F*, posterior view of condyles of: *A*, *Paracryptotis rex* Hibbard, left side no. 27257. *B*, *Notiosorex jacksoni* Hibbard, right side no. 24354. *C*, *Blarina adamsi* Hibbard, right side no. 24352. *D*, *Cryptotis? meadensis* Hibbard, left side no. 27266. *E*, *Sorex rexroadensis* Hibbard, left side no 28147. *F*, *Paracryptotis rex* Hibbard, left ramus no. 27257, lateral and occlusal views. All ×8.

(fig. 3A). The lower articular surface is large and extends under the ventral side of the condyle.

CRYPTOTIS? MEADENSIS Hibbard, n. sp.
Figures 2E, 3D

Holotype.—No. 27266, University of Michigan Museum of Paleontology; posterior part of left ramus, with P_4–M_3. Collected by Hibbard and party, summer of 1950.

Type locality.—University of Michigan locality, UM-Kl-47, in Fox Canyon, sec. 35, T. 34 S., R. 30 W., XI Ranch, Meade County, Kansas.

Age.—Upper Pliocene, Rexroad formation, Rexroad fauna.

Diagnosis.—A shrew the size of *Cryptotis parva* (Say) and intermediate in size between *Sorex taylori* and *Sorex rexroadensis*. The fourth lower premolar lacks an anterior projection that would rest on the upper surface of the canine. The tooth does not possess an excavation on the lingual occlusal surface; there is an indication of a small cusp on the posterior edge. The entoconids of M_1 and M_2 are weakly developed. The talonids of M_1 and M_2 are narrow anteriorly where they join the trigonids of the respective teeth. M_3 has a small trigonid in comparison with the heavy, rounded talonid.

Description of holotype.—P_4 is distinct in that it does not possess an anterior projection and lacks a depression on the lingual side of the crown posterior to the protoconid. A cingulum is present along the lingual and labial base of the tooth. M_1 has a large metaconid whose base extends anteriorly toward the paraconid, leaving a narrow valley which separates the paraconid and metaconid. The cusps of the paraconid, protoconid and metaconid form an equilateral triangle. A distinct labial groove is present where the talonid joins the trigonid in M_1 and M_2. The anterior labial occlusal edge of the talonids of M_1 and M_2 join the trigonids at the midline between the metaconid and protoconid. A well-developed cingulum is present along the labial side of M_1 and M_2. The cingulum is poorly developed on the lingual side. No lingual valley occurs between the paraconid and metaconid of M_3 at the base of the tooth. A slight basin exists between the paraconid, protoconid, and metaconid. The heel (talonid) of M_3 is well developed but does not show distinct cusps. It appears as though the entoconid and hypoconid have fused. The talonid is but slightly worn. The anteroposterior diameter of P_4–M_3 is 3.8 mm., of M_1 to M_3 is 3.3 mm. The alveoli of the incisor and canine are present. The posterior part of the jaw is nearly perfect.

Comparison with other forms.—The dentition of the lower jaw is distinct from that of *Sorex*, *Microsorex*, and *Notiosorex* in the reduction of cusps on the talonid of M_3. It is distinct from *Limnoecus* Stirton (1930) from the Miocene which possesses a single articular surface on the condyle. As far as is known the only genera of North American shrews which possess the reduced heel on M_3 are *Blarina* and *Cryptotis*. Since the dentition is distinct from that of the numerous specimens of *Blarina* with which it was found and because P_4 in outline is more nearly the shape of that found in the genus *Cryptotis* the jaw is questionably assigned to that genus. *Cryptotis? meadensis* is approximately the size of *C. parva*, a shrew now living in Meade County. *C.? meadensis* is distinguished by the lack of a well-developed posterior cusp on P_4 and by the absence of a slight excavation on the lingual side of the tooth.

M_1 of *C.? meadensis* is distinct in that the metaconid is broad at the base, with a very narrow valley separating the base of the paraconid from that of the metaconid. The entoconid of M_1 is not as large as that in *C. parva*. The anterior labial side of the talonid joins the trigonid much nearer the metaconid than in *C. parva*. The condition is also present in M_2.

The metaconid of M_2 is larger than that of M_2 of *Cryptotis parva*. The valley separating the base of the metaconid from the paraconid is also narrower. The entoconid of M_2 is larger and more anteriorly placed than in *C. parva*. The hypoconulid is well developed, forming the posterolingual border of the tooth. As previously noted M_3 does not possess a valley that separates the paraconid and metaconid along the lingual side of the tooth to its base as in *C. parva*. The base of the molars of *C.? meadensis* is approximately twice as thick on the lingual side below the level where the cusps originate as

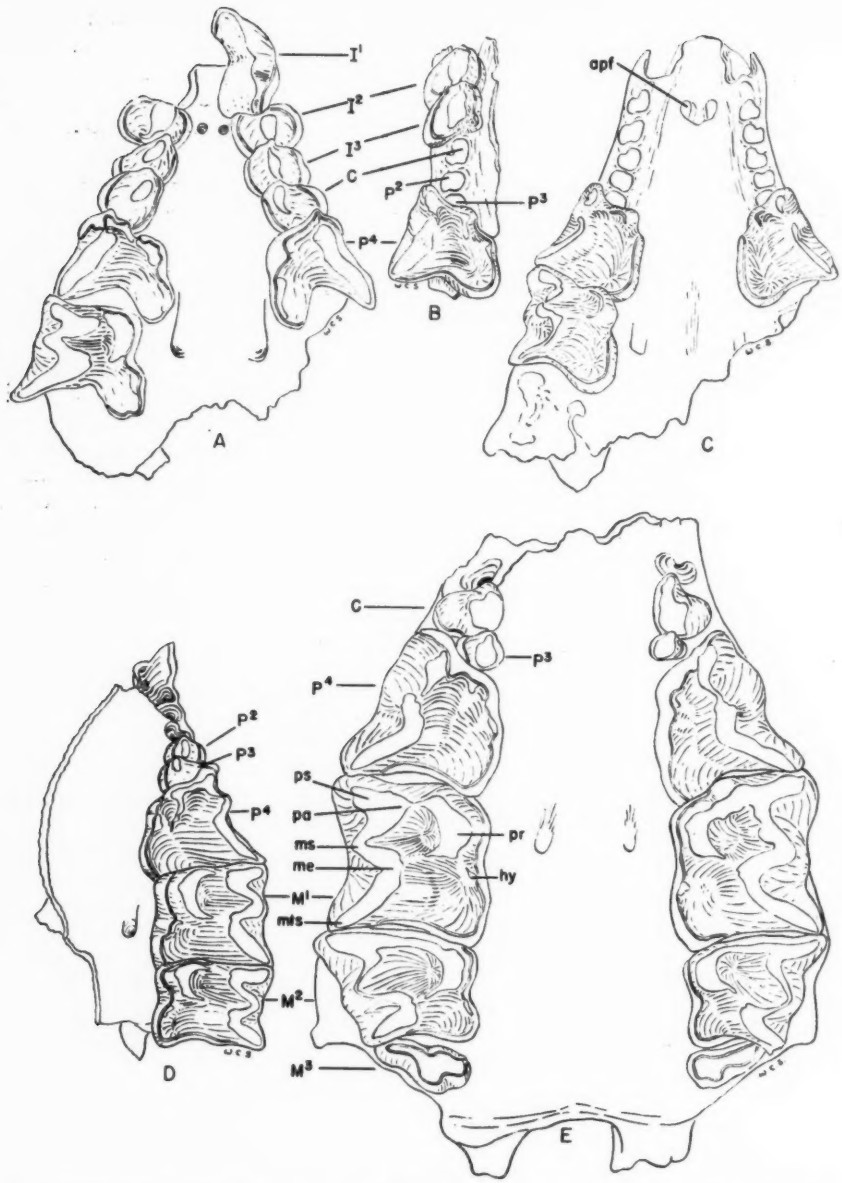


FIG. 4—*A*, *Notiosorex jacksoni* Hibbard, ventral view of palate, no. 27257. *B*, *Blarina adamsi* Hibbard, n. sp., paratype, no. 27269, ventral view of right premaxillary-maxillary. *C*, *Blarina adamsi* Hibbard, n. sp., paratype, no. 27268, ventral view of palate. *D*, *Blarina adamsi* Hibbard, n. sp., holotype, no. 27267, left premaxillary-maxillary. *E*, *Paracryptotis rex* Hibbard, ventral view of palate, no. 27209. All ×10. Abbreviations: a.p.f., anterior palatine foramen; hy., hypocone; me., metacone; ms., mesostyle; mts., metastyle; pa., paracone; pr., protocone; ps., parastyle.

in *C. parva*. The talonid of M_3 is as long anteroposteriorly as the trigonid. The talonid is heavily developed, and rounded like the greatly reduced talonid in *Cryptotis floridana* (Merriam) and not narrowed toward the occlusal surface as in *Cryptotis parva*. The place of attachment of the muscle to the labial tip of the coronoid process is

more nearly like that observed in *C. micrura* Thomas than in the smaller forms of *Cryptotis*. The dorsal surface of the condyle of the ramus has been slightly weathered. The condyle possesses two articular surfaces (fig. 3D). The general shape of the condyle is more like that of *C. micrura* than that of *C. parva* or *C. floridana* since it does not possess as deep a concavity on the lingual side. The sigmoid notch has the general shape of that notch in *C. parva*. The angular process is nearly complete.

BLARINA ADAMSI Hibbard, n. sp.
Figures 2B; 3C; 4B, C and D; 5B

?*Sorex* sp., HIBBARD & RIGGS, in part, 1949, Bull. Geol. Soc. America, vol. 60, p. 835.
Notiosorex jacksoni HIBBARD, in part, 1950, Contrib. Mus. Paleontol., Univ. Michigan, vol. 8, no. 6, p. 131, fig. 4A.

Holotype.—Left premaxillary and maxillary, bearing P^2–M^2, no. 27267, University of Michigan Museum of Paleontology. Paratypes: no. 27268, palate, bearing RP^4–M^1 and LP^4, also alveoli of incisors and unicuspids; no. 27269, part of right premaxillary and maxillary bearing I^2, I^3 and P^4; no. 28403, anterior part of palate bearing RP^4–M^2 and LP^4, also alveoli on right side for I^1–P^2, and left alveoli for I^1–P^3; no. 27270, right premaxillary and maxillary bearing alveoli for I^1–C and P^3, with P^2 and P^4–M^2 present.

Type locality.—University of Michigan locality UM-Kl-47, in Fox Canyon, sec. 35, T. 34 S., R. 30 W., XI Ranch, Meade County, Kansas.

Age.—Upper Pliocene, Rexroad formation, Rexroad fauna.

Diagnosis.—A *Blarina* smaller than *B. brevicauda carolinensis* (Bachman) and the size of *Notiosorex jacksoni* Hibbard. *Blarina adamsi* is characterized by its small size, less developed posterior lingual cusps on I^2, I^3 and P^2. P^3 not as reduced as in *B. brevicauda carolinensis*. The groove between the protocone and hypocone of P^4–M^2 shallow, not as deep as in Recent forms.

Description of holotype.—P^2 is anteroposteriorly flattened and does not possess a small lingual cusp as in Recent forms. Reduced P^3 is just visible from labial side of maxillary. This tooth is not as small as P^3 of the Recent forms of *B. b. carolinensis* and *B. b. hulophaga* Elliot. The posterior edge of P^4, M^1 and M^2 not excavated. The teeth fit closely together. Anteroposterior length of P^2–M^2 is 4.5 mm. (fig. 4D).

This species is named for the late Alex(ander) W. Adams, who owned the land on which the quarry in Fox Canyon is located and who cooperated in every way possible to make our work in that region a success.

Description of paratypes.—Specimen no. 27268 is a young adult (fig. 4C). The cusps of the teeth are but slightly worn. The anterior palatine foramina (fig. 4C) are large and situated in a slight depression, which does not occur in Recent specimens of *Blarina* examined. The significance of this development is not known. It may have some bearing on the factor of tolerance of *Blarina adamsi*. Moojen (1948, p. 393) after the study of *Proechimys*, the Brazilian spiny rats, concluded that, "In subspecies of any one full species the incisive foramen [anterior palatine foramina] is larger in animals which inhabit arid areas than in those which inhabit humid areas." The posterior borders of the foramina are situated approximately on a line with the posterior edge of the alveoli of the second incisors. The distance between the anterointernal angles (the lingual edges of the protocones) of the fourth premolars is 1.3 mm.

Specimen no. 27269, part of the right premaxillary and maxillary, contains I^2, I^3 and P^4. I^2 is as large as I^2 in *Blarina b. carolinensis*. It has a well-developed cingulum on both the lingual and labial sides. There is no evidence of a posterointernal cusp on the cingulum. I^3 rests in a very shallow groove on the posterior part of the crown of I^2. I^3 is as large as it is in *B. b. carolinensis*, it has an indication of a posterointernal cingular cusp. The maxillary tooth row of *B. b. carolinensis* is greater in length than that of *B. adamsi*, but the anteroposterior length of the five unicuspids of the two forms are approximately the same. The anteroposterior length of I^2–P^4 is 3.5 mm.

Specimen no. 28403 is the palatal region with RP^4–M^2 and LP^4. The alveoli of RI^1–P^2 and of LI^1–P^3 are present. Right P^3 was never present. This is in contrast to a Recent specimen, no. 83451, of *B. brevicauda* in the Museum of Zoology, from Iowa, which has

a supernumerary unicuspid tooth between the LC and LP^2 (see Jackson, 1928, p. 19 for individual variation in the teeth of *Sorex*). Specimen no. 27270 is the right premaxillary and maxillary with P^2, P^4–M^1 present. Alveoli of I^1–C and P^3 present. This is the only specimen in which the posterior border of the downward projecting process of the maxillary is present. Its shape and position in relation to M^2 is the same as that in *B. b. carolinensis*. The crown of P^4 of specimen no. 27273 and the crowns of P^4–M^2 of specimen, no. 27272 are pigmented. The other specimens are discolored in fossilization and do not show the light chestnut pigmentation.

There are parts of nine individuals of *Blarina adamsi* based on the recovery of upper premolar-molar series. The greatest anteroposterior length of P^4–M^2 of seven specimens range from 4.0 mm. to 4.5 mm., average 4.21 mm.

Description of the lower jaws.—No lower jaws of *Blarina adamsi* or *Notiosorex jacksoni* were found in occlusal relationship with the maxillaries. No maxillaries of *Notiosorex* were taken until the summer of 1947, and no maxillaries of *Blarina* were recovered until the summer of 1950. Since the lower jaws of the two fossil forms are the same size, and since most of the rami recovered were fragmentary, the lower dentitions of *Notiosorex jacksoni* and *Blarina adamsi* were not at first recognized as belonging to these genera. After the genus *Notiosorex* was recognized, from maxillaries, by Hibbard (1950), he still did not understand the significance of the few rami asso-

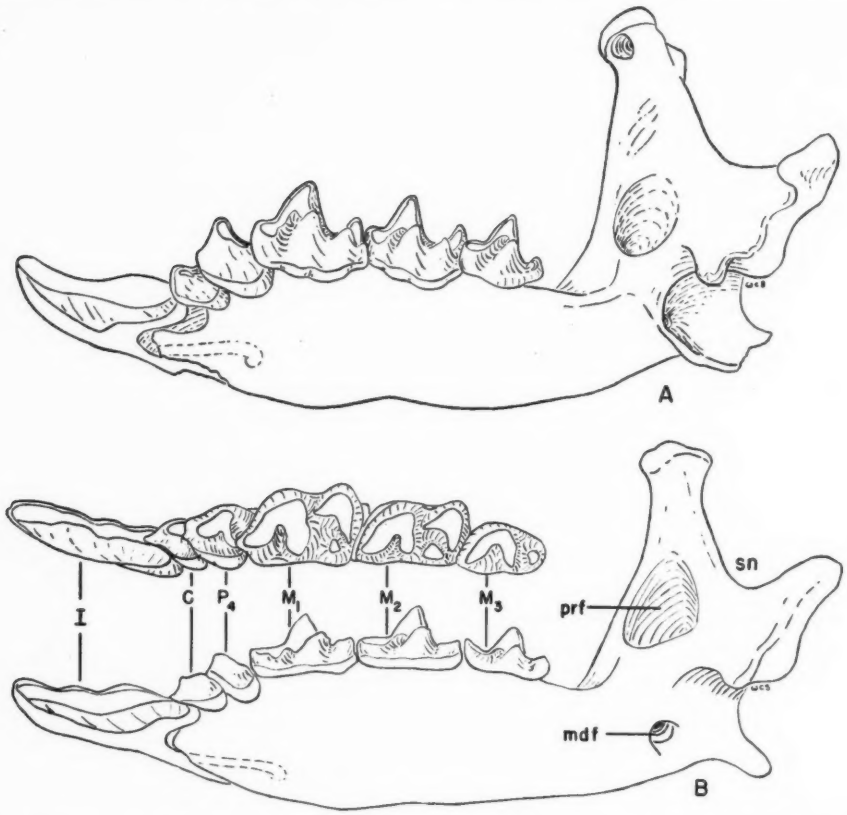


FIG. 5—*A*, *Notiosorex jacksoni* Hibbard, lingual view of right ramus, no. 24354. *B*, *Blarina adamsi* Hibbard, lingual and occlusal views of right ramus, no. 24352. All ×10. Abbreviations: mdf., mandibular foramen; prf., posterointernal ramal fossa; sn., sigmoid notch.

ciated with those of *Notiosorex* that had the area surrounding the mental foramen depressed (fig. 2B). Because of the extreme weathering of the posterior articular surfaces of the condyle, the shape of the condyle was not used as a diagnostic character until a series of perfect specimens was obtained. Unweathered condyles are more diagnostic of genera and some species than are the lower tooth patterns. Hibbard and Riggs (1949, p. 835) reported parts of two rami, nos. K.U. 7011 and K.U. 7012, from the Keefe Canyon quarry as ?*Sorex* sp. and stated that the specimens were slightly larger than *Sorex taylori*, which was previously known from the Rexroad fauna. Dr. Robert W. Wilson of the University of Kansas Museum of Natural History, has kindly compared these two rami with typical rami of *Notiosorex jacksoni* and *Blarina adamsi* and states "that specimen no. 7012 has the shape of condyle as in *Notiosorex*, not as in *Blarina*. No depression surrounding mental foramen." Also, of specimen no. 7011, "No condyle preserved in this specimen. A depression in ramus surrounding the mental foramen." The posterior part of a ramus, no. 25777 U.M.M.P., recovered September, 1948, by me from the old quarry dump at the Keefe Canyon quarry, containing M_1–M_3, possesses a good depression around the mental foramen, being chiefly in the anterior region of the foramen, and has a typical shaped condyle of *Blarina*. It is a good specimen of *Blarina adamsi*.

The character of the mental foramen and the shape of the two articular surfaces on the condyle (fig. 3B and C) of the lower jaw have been used to separate *Blarina adamsi* from *Notiosorex jacksoni*. The characters used to separate the fossil forms are also characters diagnostic of the Recent species, *Notiosorex crawfordi* Baird, and those of the genus *Blarina*. The posterointernal ramal fossa is more rounded in appearance in *Notiosorex jacksoni* than in *Blarina adamsi* (see figs. 5A and B).

In perfect specimens, the premolar-molar series is slightly longer in *B. adamsi* than in *N. jacksoni*. The cingulum is better developed in *adamsi*, especially on the base of P_4. In unworn dentitions P_4 is distinct in the two forms, being slightly longer and curving more posteriorly at the crown toward M_1 in *N. jacksoni* than in *B. adamsi*. There is evidence of a very small posterior lobe, a large median lobe, and a very small anterior lobe on the elongated incisor in a few of the specimens of *B. adamsi*.

The coronoid process does not slope anteriorly as much in *B. adamsi* as in *N. jacksoni*. The sigmoid notch (fig. 5B) is larger in *N. jacksoni*. The attachment of the muscle to the external tip of the coronoid process is distinct in the two forms (see figs. 2B and C).

Six lower jaws contain the last third molar which is unworn. The unworn heel is bladelike and centrally located in relation to the trigonid.

A few of the specimens show a slight pigmentation on the crowns of the lower teeth.

In the collection there are 30 left rami and 38 right rami of *Blarina adamsi*. The greatest anteroposterior length of M_1–M_3 of 41 specimens, range from 3.7 mm. to 4.9 mm., average 3.91 mm. The greatest anteroposterior length of C–M_3 of eight specimens, range from 4.95 mm. to 5.3 mm., average 5.14 mm.

NOTIOSOREX JACKSONI Hibbard
Figures 2C, 3B, 4A, and 5A

Notiosorex jacksoni HIBBARD, 1950, Contrib. Mus. Paleontol., Univ. Michigan, vol. 8, no. 6, pp. 129–133, figs. 2B and 4B.

?Sorex sp. HIBBARD & RIGGS, in part, 1949, Bull. Geol. Soc. America, vol. 60, p. 835, fig. 1J.

In the material recovered from the Fox Canyon deposit there are parts of 19 individuals of *Notiosorex jacksoni* based on left maxillaries, and 50 individuals based on right rami.

The upper teeth and parts of skulls recovered correspond in character with those of the holotype. All stages of tooth wear are represented. There is a faint trace of pigment on the tip of the cusps of P^4 and M^1 of specimen no. 27265. The range in maximum anteroposterior length of P^4–M^2 in ten specimens is, 4.15 mm. to 4.4 mm., average 4.27 mm.

Fifty right rami and 48 left rami of this shrew were recovered. In the material from Fox Canyon there are 79 fragmentary rami that are so broken or weathered that it is impossible to assign them either to *Blarina* or to *Notiosorex*.

The lower jaw of *Notiosorex jacksoni* is

distinguished from that of *Blarina adamsi* with which it was found by its distinctive articular condyles (fig. 3B). A distinct concavity separates the upper and lower articular surfaces on the lingual side. The lack of a depression around the mental foramen in *Notiosorex* is a distinctive character as well as is the muscle attachment on the external tip of the coronoid process (fig. 2C).

Only two lower dentitions were recovered that showed pigmentation of the teeth. In both specimens the pigmentation was very faint and confined to the extreme tips of the incisor, canine, and premolar.

In 17 specimens the range in maximum length of C–M_3, was 4.7 mm. to 5.15 mm., average 4.99 mm. In 66 specimens the range in maximum length of M_1–M_3 was 3.7 mm. to 4.1 mm.; average 3.9 mm.

This species was named for Doctor Hartley H. T. Jackson who has devoted much of his life's work to the study of Recent North American shrews and who has kindly helped in my study of fossil shrews. This statement was deleted by error from the original publication.

Discussion.—The geographical distribution of the shrews was considerably different during the upper Pliocene in the High Plains region than at present. Furthermore the ecological niches of *Notiosorex* and *Blarina* appear to be more restricted now than then. This can be due either to the extinction of certain species with wider tolerance range during the Pleistocene or to a tolerance restriction developed in one or both genera, in part, during the Pleistocene. Recent specimens of *Notiosorex* are poorly known in museum collections. No study to date of owl pellets has produced any great number of *Notiosorex* remains and no study in the field has indicated such abundance of Recent *Notiosorex* in any area within its range as is indicated during the upper Pliocene from the number of specimens recovered in Fox Canyon. *Notiosorex* is the most common shrew in the deposit and *Blarina* the next in abundance. Until recently the geographical range of the two shrews has been considered distinct. Sealander (1952) reports the presence of *Notiosorex crawfordi* from Crawford County, Arkansas. This extension of the range of *Notiosorex* northeastward, now overlaps the westward known range of *Blarina*.

If it is possible to use the information known in regard to the present habits of *Notiosorex* and *Blarina*, it would be possible to assume that *Blarina* during the upper Pliocene inhabited the more moist lowland areas and *Notiosorex* inhabited the drier hillsides, slopes and, in part, the upland areas.

MANUSCRIPT RECEIVED JANUARY 21, 1952

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO, 1, PP. 33–48, PLS. 5–8, 1 TEXT FIG., JANUARY, 1953

OBSERVATIONS ON THE TRILOBITE *CERAURUS*

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ABSTRACT—Certain misconceptions of the type species of *Ceraurus*, *C. pleurexanthemus* Green, from the Trentonian of the Mohawk Valley of New York are corrected. The strongly divergent genal spines and the low vertical angle of the great pygidial spines are the result of post-depositional flattening in specimens upon which a concept of the species has come to be based. A new variety, *C. pleurexanthemus* var. *montyensis* is distinguished on the basis of silicified remains etched from Trentonian limestone from Clinton County, N. Y. Silicified specimens from the Trentonian of the Shenandoah Valley of Virginia previously referred to the type species by Whittington, are recognized as a new species, *C. whittingtoni*. The silicified remains of the two species are compared in detail. Pits on the glabella and markings in the preglabellar furrow which are present in these three representatives of the genus *Ceraurus* are described and interpreted as points of attachment for cephalic muscles. Study of a large number of transitory pygidia of the new variety gives additional information on the ontogeny of *Ceraurus*. The segments of the transitory pygidium do not develop with equal rapidity, but the posterior thoracic segments are retarded in their growth. The pleurae of the posterior thoracic segments develop later than their axial portions. Evidence that more than one moulting took place within one meraspid degree is furnished by variations in the development of the pleurae of the posterior thoracic segments. Both the transitory pygidium taken as a whole, and the part destined to become the holaspid pygidium, increase in size in successive meraspid degrees. This is at variance with the condition in a genus very similar to *Ceraurus*.

INTRODUCTION

DURING the past dozen years the work of Whittington (1941, 1949) and, more recently, of Ross (1951 a, b) and Evitt (1951) on Lower and Middle Ordovician silicified trilobites has yielded a large number of specimens of unparalleled quality of preservation representing many species and genera. Study of this material is showing us much about trilobite ontogeny and the morphology of the trilobite exoskeleton which could not be gleaned from calcareous specimens as usually preserved. However, the very perfection of the preservation of the silicified material has made it difficult to make detailed comparisons with calcareous specimens of similar species. Work completed and in progress by the writers mentioned above covers parts of the Lower Ordovician of Utah and the Middle Ordovician of the Appalachian Province in Virginia.

Accounts of silicified trilobites published to date have not treated of specimens recovered from strata of closely similar ages in different areas. Etching of Middle Ordovician Trentonian limestones from Clinton County, in northeastern New York, has recently yielded numerous silicified specimens referable to the genus *Ceraurus* Green, 1832. These strata are approximately the same age as the source of the silicified specimens of *Ceraurus* described by Whittington (1941) from the Shenandoah Valley in Virginia, as well as of strata at the famous collecting localities for non-silicified fossils in the vicinity of Trenton Falls, New York.

In addition to naming one new variety and one new species of *Ceraurus*, the purpose of this paper is threefold: 1) to point out some misconceptions regarding *Ceraurus pleurexanthemus* Green, 2) to make a detailed comparison of the silicified examples of *Ceraurus* from New York and Virginia with each other and, where pertinent, with well preserved calcareous specimens of *Ceraurus pleurexanthemus* from the Mohawk Valley, 3) to present some additional data on the ontogeny of *Ceraurus* based on the Clinton County material.

The descriptive terminology employed is that used previously by me (Evitt, 1951).

LOCALITIES

Mohawk Valley locality (*Locality 1*). Trentonian outcrops are widespread in the Mohawk and Black River Valleys of New York. Probably the best known locality, the type Trentonian at Trenton Falls, Herkimer County, exposes the middle Trentonian Sherman Fall formation comprising the Shoreham member below and the Denmark member above (Kay, 1937). The calcareous specimens of *Ceraurus pleurexanthemus* considered in the present paper all hail from "Trenton Falls" with no more precise stratigraphic data and are in the collections of the Museum of Comparative Zoölogy at Harvard University and the New York State Museum.

Silicified trilobites also occur at Trenton Falls (Waering, personal communication). Some of these were recovered in the course of etching for arenaceous Foraminifera. Waering (1934) reported the occurrence of Foraminifera only, but at least the trilobite genus *Diacanthaspis* is represented among specimens which he sent to the New York State Museum (Whittington, personal communication). No further etching of blocks from this locality has been accomplished to date.

Shenandoah Valley locality (*Locality 2*).—The specimens of *Ceraurus whittingtoni* Evitt, n. sp., described and discussed in this paper are from blocks collected at a hillside exposure about 300 yards northwest of the junction of Augusta County roads 752 and 753 and about 4 miles north-northeast of Spring Hill, Augusta County, Virginia. Other trilobites recovered include *Flexicalymene senaria* (Conrad), abundant *Cryptolithus tesselatus* Green, and the genera *Isotelus* and *Calliops*.

The silicified Trentonian trilobites discussed by Whittington (1941) were derived from a locality about 1.5 miles closer to Spring Hill along the strike from my Locality 2. Whittington (1941, p. 492) alluded to two localities, one near Spring Hill and a second near Long Glade. Since Spring Hill is a newer name for the settlement formerly called Long Glade, Whittington (personal communication) believes that all of his material probably came from one locality. The trilobite assemblage recovered by Whittington differs slightly from that of my Locality 2 but the dominant elements are the same: *Cryptolithus tesselatus* Green, *Flexicalymene senaria* (Conrad) and a species of *Ceraurus* which I believe to be conspecific with *C. whittingtoni*. Whittington characterizes the age of the strata yielding his material as "possibly the same as that of the Denmark member of the Sherman Fall formation." Although *Cryptolithus tesselatus* is reported by Kay (1937, p. 267) as a guide fossil of the Shoreham member beneath the Denmark in New York, its occurrence in Virginia has not been so exactly determined.

Clinton County locality (*Locality 3*).—The exposure which has yielded the first silicified trilobite remains to be described from the New York Trentonian is, oddly enough, located west of Lake Champlain in Clinton County, the classic area for the Chazyan, and not in the classic Trentonian section of the Mohawk Valley southwest of the Adirondacks. The outcrop is a single small one, exposed in a deep drainage gutter along the south side of the road from the town of Chazy to Chazy Landing on Little Monty Bay, and about 0.25 mile west of Chazy Landing. The strata are dark, argillaceous limestones with thin shale layers between, some bedding surfaces replete with *Resserella* sp. The precise geologic horizon represented is not known. The area has not been mapped in general, although Oxley (1950) has dealt with the Chazyan of the immediate vicinity. The genus *Ceraurus* is abundantly represented and, in addition, there occur the genera *Flexicalymene, Isotelus, Calliops, Calyptaulax. Leonaspis?*, and *Diacanthaspis. Cryptolithus tesselatus* has not been encountered. Oxley (personal communication) remarks that, upon cursory examination by him, the strata exposed here seem similar in lithology to the Cumberland Head formation, i.e. Denmark equivalent in the Champlain Valley section.

Although this exposure is of more recent date, P. E. Raymond in 1919 (Whittington, personal communication) collected a loose block of limestone from "Little Monty Bay, Chazy, New York" which yielded silicified specimens of *Flexicalymene* upon etching. These are in the collections of the Museum of Comparative Zoölogy and are treated in another study (Evitt and Whittington, this issue). Probably this was an isolated block

from the immediate vicinity of the locality mentioned above.

Relative ages of localities.—From these remarks it will be seen that, according to the best information available at the present time, the three localities involved expose approximately contemporaneous strata (middle Trentonian), although with present means it would be impossible to prove absolute synchroneity.

SYSTEMATIC PALEONTOLOGY

Family CHEIRURIDAE Hawle and Corda, 1847

Genus CERAURUS Green, 1832

CERAURUS PLEUREXANTHEMUS Green, 1832

Plate 5, figures 1–8; plate 7, figures 1, 2; plate 8, figures 5–7; text-fig. 1a

Ceraurus pleurexanthemus GREEN, 1832, Monthly Jour. Geol., pl., fig. 10.

Ceraurus pleurexanthemus GREEN, 1832, Monograph of the trilobites of North America, pl.84, pl. 1, fig. 10.

Ceraurus pleurexanthemus Green. RAYMOND, P. E., and BARTON, D. C., 1913, A revision of the American species of *Ceraurus:* Bull. of Mus. Comp. Zoöl., vol. 54, no. 20, pp. 528–533, pl. 1, fig. 1; pl. 2, figs. 1, 2, 7; text-figs. 1–3.

non *Ceraurus pleurexanthemus* Green. WHITTINGTON, H. B., 1941, Silicified Trenton Trilobites: Jour. Paleontology, vol. 15, pp. 498–502, pl. 73, figs. 1–40; text-figs. 7, 8, 11–13.

Holotype.—NYSM 4203, a partially covered and flattened entire specimen.

Locality and horizon.—Newport, Herkimer County, New York (Locality 1); middle Trentonian.

Among American paleontologists the name of this species is one of the best known of trilobites. It has been reported from multitudinous Blackriveran and Trentonian exposures in eastern North America. Only three specific items are cited from its extensive synonymy. These include its original description and an illustration (without description) published earlier in the same year by Green, a redescription and discussion by Raymond and Barton, and a discussion of a form referred to this species by Whittington which is distinguished below as a new species, *C. whittingtoni.*

The type specimen of *C. pleurexanthemus* was figured in drawings by Green and by Hall (1847) and for the first time (to my knowledge the only time) in a photograph by Ruedemann (1912). Because of the inaccessibility of the last publication the type is here refigured (pl. 5, fig. 1). Unfortunately it is very poorly preserved. About all it shows is a trilobite with 11 thoracic segments bearing diagonal pleural furrows, a pygidium with one long side spine of a pair, and a cranidium with a long genal spine, a glabella with three pairs of lateral lobes (the first separated from the median lobe of the glabella by a furrow), a pair of prominent and high eyes far out on the cheeks, and two tubercles on the left cheek inside the eye. Other details are obscured by matrix or exfoliation and the specimen has been somewhat flattened. The type rests in the New York State Museum and is from Newport, Herkimer County, New York. Exposures along Rathbone Brook, a mile northwest of the village of Newport reveal beds of the upper Hull and Sherman Fall formations, while closer to town occur lowermost Trentonian and Blackriveran outcrops (Kay, 1937). Thus, the exact stratigraphic source of the type specimen must remain in doubt. Raymond and Barton (1913, p. 259) even remark "that the original specimen may have come from Trenton Falls." At least they were convinced, and it seems justifiably so to me, that the characters of the type are "in accord with the specimens from that locality [Trenton Falls]" and that "in any case, specimens from Trenton Falls may be taken as typical of the species." Their redescription of the species is based on specimens found at Trenton Falls.

From the many occurrences of species of the genus *Ceraurus* in North America and Europe it is well known that the cephalon characteristically exhibits moderate longitudinal and transverse convexity with the fixed and free cheeks falling off steeply outside the eyes. Furthermore, the outer parts of the anterior thoracic pleurae are bent strongly downwards. Thus, a transverse section through the posterior part of the cephalon or one of the anterior segments has a nearly horizontal portion adjoining the axial furrow and then arches downward as the genal angle or pleural tip is approached. Most of the specimens in the collections at the Museum of Comparative Zoölogy which were studied by Raymond and Barton do not show this. Rather, as

suggested by their plates and as shown on pl. 5, fig. 5 of this paper, the cheeks are relatively flat and the posterior portion horizontal, so that, except for the occipital ring, the whole posterior margin of the head between the genal angles is nearly in a plane. The longitudinal convexity of the glabella is also less than usual, and the long terminations of the anterior thoracic segments are stretched out flat.

The typical specimens from Trenton Falls and the most complete specimens in the Museum of Comparative Zoölogy collections are preserved in thin-bedded, very argillaceous limestone. Herein lies the explanation of the lessened convexity of these specimens. It seems that compaction of the sediments was accompanied by a moderate flattening of the fossils. This was not severe enough to result in gross distortions of the trilobites (cracks are visible in some, but not all cases), and does not seem to have affected at all the more sturdy skeletal remains of such organisms as brachiopods and crinoids, but the stresses were sufficient to affect the more convex parts of the *Ceraurus* exoskeletons to a noticeable degree. This interpretation is substantiated by the fact that the Trenton Falls section does contain some beds of less argillaceous and finely crystalline limestone and specimens of *C. pleurexanthemus* in such material retain their full convexity.

This circumstance has some consequence when one considers its effect on the outline of the cephalon which plays an important role in the determination of a genus or species of trilobite. Raymond and Barton's drawing (1913, pl. 1, fig. 1) shows an admirable representation of the cephalon of the specimen here illustrated as pl. 5, fig. 5. Two outstanding features of the cephalic outline to be noted are the rounded anterolateral "corners" determined by the margins of the free cheeks, and the strongly divergent genal spines. Comparison of many specimens in the Museum of Comparative Zoölogy collections and elsewhere has convinced me that both these features are the result of an outward rotation and flattening of the originally steep outer cheek regions as the highly argillaceous sediments were compacted. If this conclusion is correct, then, of course, these features are not ones upon which to base comparisons with other species of the genus.

Except for failing to recognize this flattening of specimens, Raymond and Barton's redescription of the species is satisfactory. However, several other points which have important bearing on the description of the new variety and new species below should be noted here.

1. The eye lobes in this species are very high. This feature is difficult to observe because of their exposed position and consequently infrequent preservation. However, the specimen illustrated in Raymond and

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EXPLANATION OF PLATE 5

FIG. *1*—*Ceraurus pleurexanthemus* Green. Stereograph of the type specimen, NYSM 4203, ×1.5. The specimen has been flattened, is partly exfoliated and the marginal portions are covered with matrix. Locality 1, near Newport, N. Y. (p. 35)

2, *6*, *7*—*C. pleurexanthemus* Green. An uncrushed specimen, MCZ 5097. *2*, oblique view of glabella showing incompleteness of second glabellar furrow, ×3; *6*, detail of anterior slope of frontal lobe of glabella and adjoining furrow and anterior border, showing muscle marks, ×9; *7*, detail of left free cheek, showing inflated upper portion of ocular platform, ×5. Locality 1, Trenton Falls, N. Y. (p. 35)

3–5, *8*—*C. pleurexanthemus* Green. The specimen (MCZ 4) illustrated by Raymond and Barton, 1913, pl. 2, fig. 1. *3*, anterior view of right eye, ×4; *4*, detail of right eye and free cheek, ×8; *5*, stereograph of cephalon with widely divergent genal spines resulting from flattening, ×2.5; *8*, oblique view of cephalon, showing cheek, eye and eye ridge, ×3.5. Locality 1, Trenton Falls, N. Y. (p. 35)

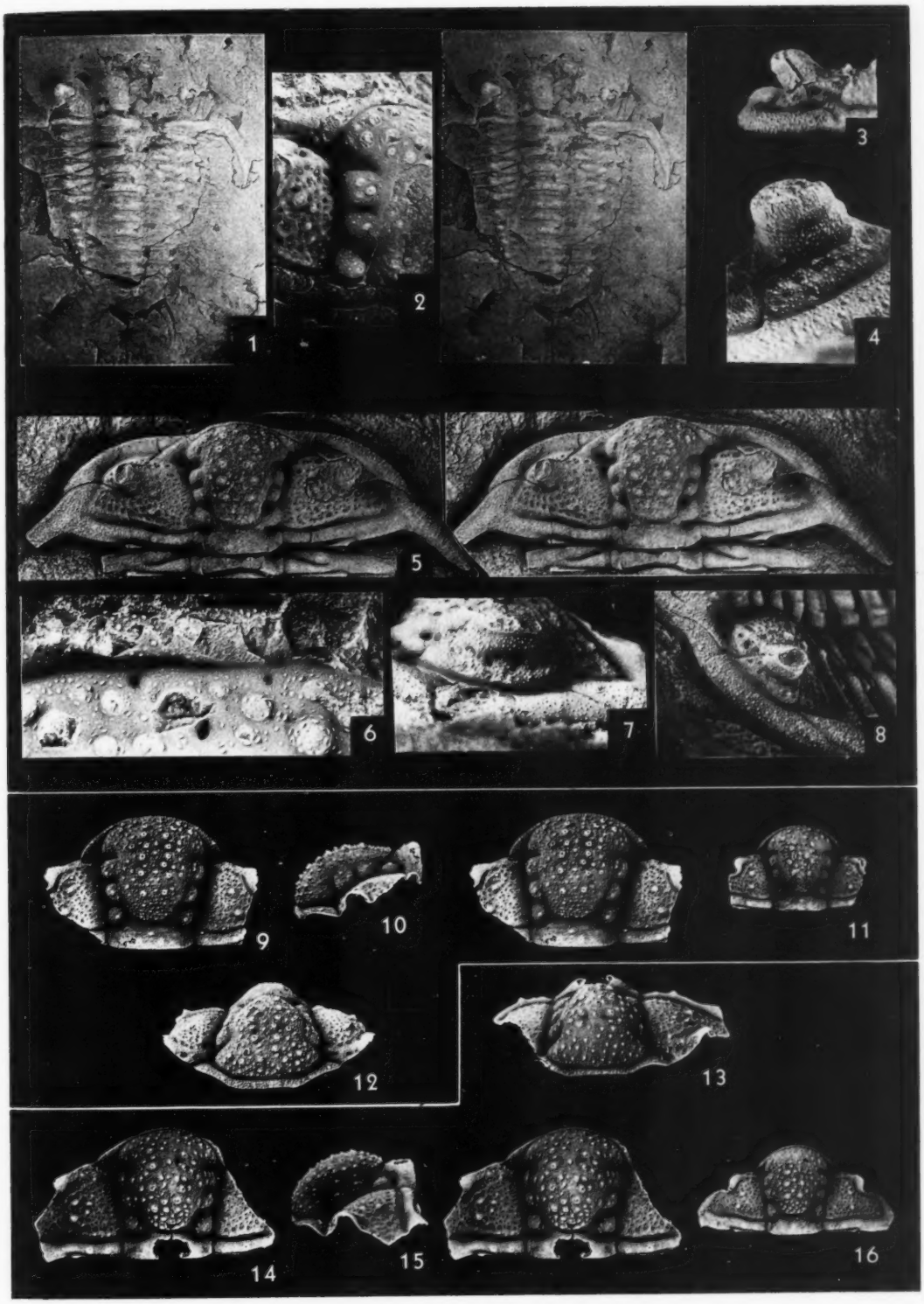
9, *10*, *12*—*C. pleurexanthemus* var. *montyensis* Evitt, n. var. A fragmentary cranidium. *9*, dorsal stereograph; *10*, left lateral view; *12*, anterior view; ×2.5. Locality 3.

11—*C. pleurexanthemus* var. *montyensis* Evitt, n. var. Fragmentary cranidium, dorsal view, ×2.5. Locality 3. (p. 38)

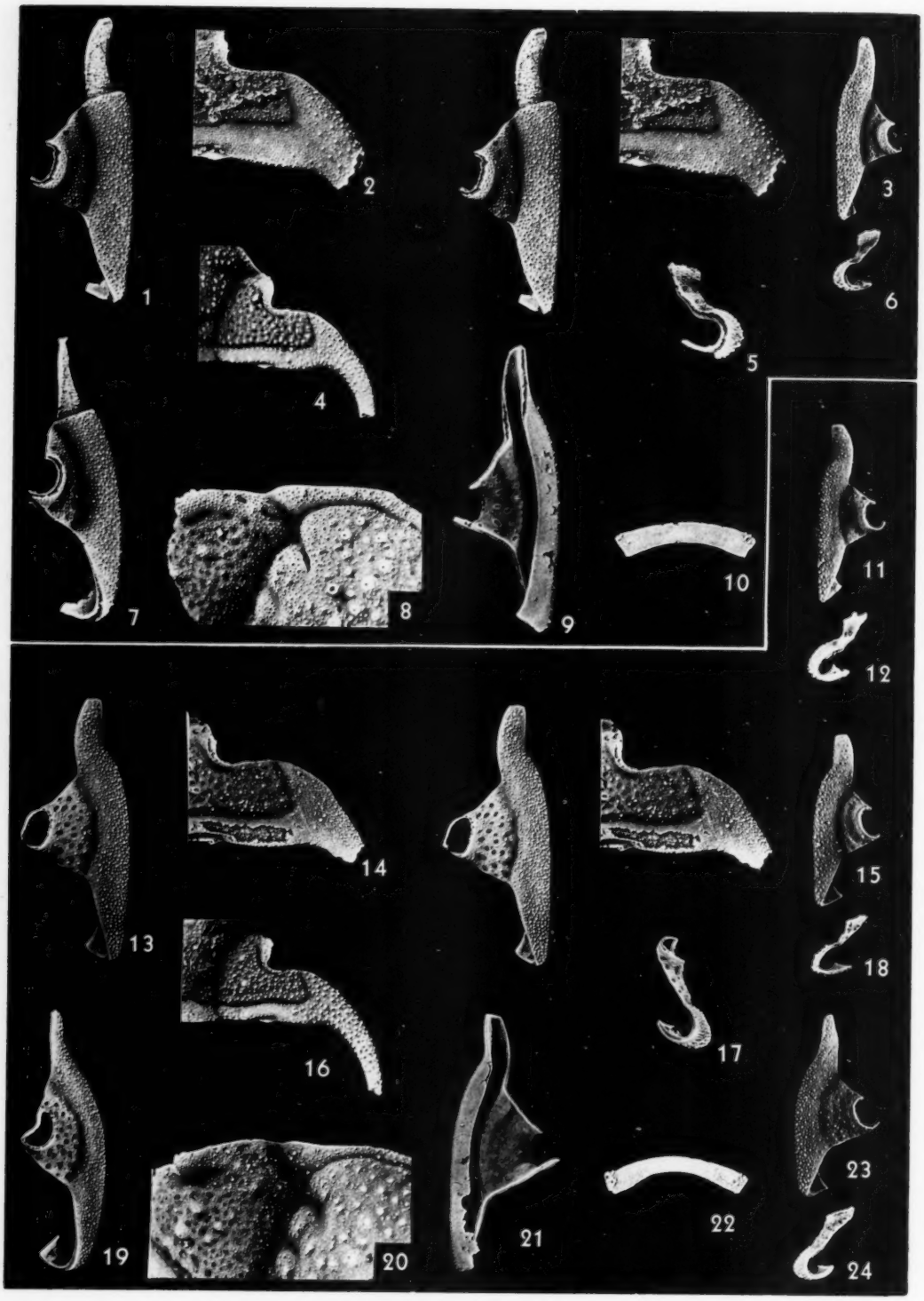
13–15—*C. whittingtoni* Evitt, n. sp. Fragmentary cranidium. *13*, anterior view; *14*, dorsal stereograph; *15*, left lateral view; ×2.5. Locality 2. (p. 39)

16—*C. whittingtoni* Evitt, n. sp. Fragmentary cranidium, dorsal view, ×2.5. Locality 2. (p. 39)

Note—Figs. *1–8* are calcareous specimens, figs. *9–16* are silicified.



Evitt, Ordovician trilobite *Ceraurus*



Evitt, Ordovician trilobite *Ceraurus*

Barton's pl. 2, fig. 1 shows them to perfection (pl. 5, figs. 3, 4). The palpebral lobes are large and incline outward and forward. The eye surface itself is not unusual in size but surmounts a distinctively inflated, short, broad eye stalk on the free cheek. Unlike the flat ocular platform below it, this inflated region is without pits and is ornamented only with fine tubercles and granules (pl. 5, figs. 4, 7).

2. The second glabellar furrow, at its junction with the axial furrow, is noticeably less developed than either the first or the third. In some specimens this furrow consists of a deep, elongate pit nearly isolated from the axial furrow (pl. 5, fig. 2). There is, however, considerable variation in this feature, but the tendency toward incomplete development of the second furrow is common to all three of the forms of *Ceraurus* considered in this paper.

3. The genal spines and the great pygidial spines in this species are circular in cross-section. Similarly, the outer surfaces of the lateral borders of the cheeks are semicircular rolls.

4. The two great spines of the pygidium in this species arise at a considerable angle to the general surface of the pygidium between them. This is difficult to ascertain because, like the lateral portions of the cephalon, these spines have been deformed in many specimens so that they seem to lie in about the same plane as the rest of the pygidial surface. However, several undeformed specimens show their inclination.

5. The posterior margin of the pygidium in this species shows considerable variation, as analyzed by Raymond and Barton (1913). Between the great spines the margin may be a nearly smooth curve or bear up to four short, rounded prominences (called "spines" by Raymond and Barton). Their line drawings are somewhat generalized and misleading and photographs of the examples which they selected to illustrate this variation are here presented (pl. 8, figs. 5–7) for comparison with the new variety described below.

6. Whittington noted (1941, p. 499) that Raymond and Barton figured but did not describe the hypostome of *C. pleurexanthemus*. Although Whittington's description of the hypostome applied to *C. whittingtoni* and not to *C. pleurexanthemus*, it is not felt necessary here to offer a complete description of the hypostome of the latter. The specimens of hypostomes which I have seen from Trenton Falls seem to agree in all respects with Whittington's description if it is amended to read "with distinct maculae" instead of "without maculae." Raymond and Barton's figure (1913, pl. 2, fig. 7) is of an imperfectly preserved specimen and is supplemented here with pl. 7, figs. 1, 2.

7. Pits on the glabella and markings in

EXPLANATION OF PLATE 6

Ceraurus pleurexanthemus var. *montyensis* Evitt, n. var. Locality 3. (p. 38)

FIGS. *1, 5, 7*—Free cheek; exterior stereograph, posterior profile and dorsal view, ×4.5.
2—Stereograph of genal angle of a fragmentary cranidium, ×7.
3, 6—Free cheek, exterior view and posterior profile, ×4.5.
4—Genal angle of a fragmentary cranidium, ×9.
8—Cranidium, oblique view showing left palpebral lobe, eye ridge, and part of glabella, ×5.
9—Free cheek, interior view, ×4.5.
10—Rostrum, exterior view, ×7.

Ceraurus whittingtoni Evitt, n. sp. Locality 2. (p. 39)

FIGS. *11, 12*—Freek cheek, exterior view and posterior profile, ×3.5.
13, 17, 19, 21—Free cheek. *13*, exterior stereograph; *17*, posterior profile; *19*, dorsal view; *21*, interior view; ×4.5.
14—Stereograph of genal angle of a fragmentary cranidium, ×7.
15, 18—Free cheek, exterior view and posterior profile, ×3.5.
16—Genal angle of a fragmentary cranidium, ×9.
20—Fragmentary cranidium, oblique view, showing left palpebral lobe, eye ridge and part of glabella, ×5.
22—Rostrum, exterior view, ×7.
23, 24—Free cheek, exterior and posterior profile, ×4.5.

Note—All specimens are silicified.

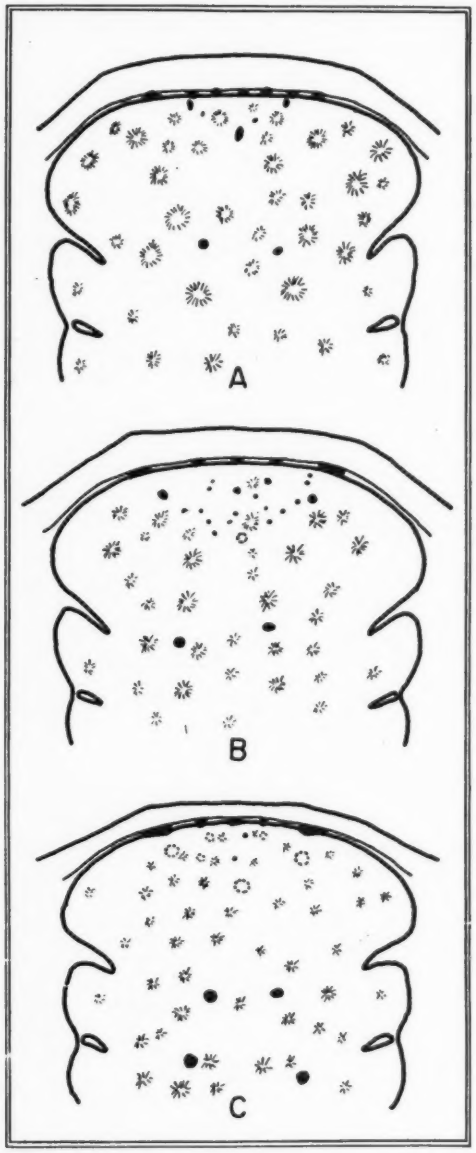


FIG. 1—Muscle attachments. Schematic diagrams of the anterior border, preglabellar furrow and anterior portion of the glabella to show the distribution of markings interpreted as points of muscle attachment. Pits on the glabella are indicated in solid black, localized depressions by broken, open circles. Areas in the preglabellar furrow are in solid black. The larger tubercles of the surface ornament are suggested by hachures.

A. *Ceraurus pleurexanthemus* Green

B. *C. pleurexanthemus* var. *montyensis* Evitt, n. var.

C. *C. whittingtoni* Evitt, n. sp.

Diagram A is based on a single specimen; B and C suggest the variable extent to which the pits are developed and do not represent particular specimens.

the preglabellar furrow interpreted as points of muscle attachment—see below, under Muscle Marks, for discussion.

CERAURUS PLEUREXANTHEMUS var. MONTYENSIS Evitt, n. var.

Plate 5, figures 9–12; plate 6, figures 1–10; plate 7, figures 3, 5–12, 21–28; plate 8, figures 1–4, 8–16; text-figure 1b

Holotype.—USNM 116693-a, an incomplete silicified pygidium.

Paratypes.—USNM 116693-b to -z, an assortment of disassociated parts of the exoskeleton.

Locality and horizon.—Little Monty Bay, near Chazy, Clinton County, New York (Locality 3); Trentonian.

This variety agrees generally with typical specimens of *C. pleurexanthemus* from Trenton Falls when allowance is made for the flattening of many of those specimens as noted above. The two salient points on which the varietal distinction is made are:

1. The eye is not so high. The palpebral lobe is smaller and the inflated eye-stalk on the free cheek is lower (cf. pl. 5, fig. 3, vs. pl. 5, fig. 12 and pl. 6, fig. 5).

2. The pygidial outline, exclusive of the great spines, is strongly subtriangular (pl. 8, fig. 8) in contrast to rounded or subsemielliptical. As with the Trenton Falls specimens there is considerable variation in the posterior margin between the two great spines but in general the margin extends farther back at the midline and the second, third, and rudimentary fourth segments of the pygidium tend to develop much more distinct, rounded prominences. The characteristic appearance is shown in the holotype, pl. 8, fig. 8, while on pl. 8, figs. 11–14 illustrate the range of variation.

Muscle marks on the cranidium are discussed in a separate section below. Other features which are known from the silicified material but which have not been described for *C. pleurexanthemus* itself are the rostrum and the presence of perforated tubercles and

other perforations through the exoskeleton.

Rostrum.——(pl. 6, fig. 10). This is a subrectangular plate with a moderate and unequal arcuation of the two longer sides, the stronger arc being the hypostomal suture. The connective sutures meet the hypostomal and rostral sutures nearly at right angles. The width (tr.) is about seven times the sagittal length. The length (exs.) at the connective sutures is somewhat greater. The shape and size of this plate is subject to some variation.

Perforations.——Perforations through the exoskeleton are now known to occur in many trilobites (Shirley, 1936; Whittington and Evitt, in two papers, one in this issue). These have been interpreted as the loci of sensory hairs. In *C. pleurexanthemus* var. *montyensis* some perforations of this sort penetrate the larger tubercles of the exterior surface (shown clearly on the glabella in pl. 6, fig. 8), while others are located among the elements of the granular ornament and not on discrete tubercles. Examples of the latter are the tips of the thoracic pleurae (pl. 8, fig. 4) and the border of the free cheek (pl. 6, fig. 1).

The new variety is fully illustrated here because of the fine preservation of detail in the silicified specimens recovered. This gives a clearer picture of some of the characteristics of *C. pleurexanthemus* itself, to which the variety is closely similar, and also affords grounds for a careful comparison with silicified specimens of *C. whittingtoni*, n. sp., from Virginia.

CERAURUS WHITTINGTONI Evitt, n. sp.
Plate 5, figures 13–16; plate 6, figures 11–24; plate 7, figures 4, 13–20; plate 8, figures 17–25; text-figure 1c

Ceraurus pleurexanthemus Green. WHITTINGTON, H. B., 1941, Silicified Trenton trilobites; Jour. Paleontology, vol. 15, pp. 498–502, pl. 72, figs. 1–3, 9–40; text-figs. 7, 8, 11–13.

Holotype.—USNM 116692-a, an incomplete pygidium.

Paratypes.—USNM 116692-b to -z, an assortment of disassociated silicified parts of the exoskeleton.

Locality and horizon.—Four miles north-northeast of Spring Hill, Augusta County, Virginia (Locality 2); Middle Trentonian.

In addition to the material discussed below, I also refer to this species the specimens described and figured by Whittington (1941) with the exception of those figured on his plate 72, figs. 4–8. These excepted specimens are characterized by a coarser ornament and higher palpebral lobes as noted by Whittington (1941, p. 499), and in these respects are similar to *C. pleurexanthemus* Green.

Whittington's failure to recognize the differences which set *C. whittingtoni* specifically apart from *C. pleurexanthemus* is readily understandable in the light of three considerations. First, the holotype of *C. pleurexanthemus* is unsuitable for detailed comparison with other specimens. Second, the general exoskeletal structure of the two species is quite similar. Third, as a result of post-depositional flattening, two of the most distinctive features of *C. whittingtoni* as discussed below (flattened cross-sections of borders and spines and the low vertical angle of the great pygidial spines) are, indeed, simulated by many of the Trenton Falls specimens of *C. pleurexanthemus* which have served as a "standard of reference" for that species.

The following description is presented in the form of an analysis of differences between *C. whittingtoni* and *C. pleurexanthemus* var. *montyensis* based on silicified specimens from Localities 2 and 3, respectively. As far as I can tell after close study, all of the distinctions apply as well when *C. whittingtoni* is compared with *C. pleurexanthemus* itself. The flattened cross-sections of borders and spines distinguish *C. whittingtoni* from other species of the genus known to me.

The plates are arranged to facilitate visual comparison between *C. whittingtoni* and *C. pleurexanthemus* var. *montyensis* in conjunction with the remarks below. Therefore, numerous specific references to plates and figures are omitted. The distinctions are discussed in order of decreasing ease of observability under the headings of each exoskeletal part.

Cranidium.—Next to the thoracic segments the cranidia of the two species show the least difference. This is interesting since it is usually in the cranidia of trilobites that distinguishing features are first looked for. 1. The border of the cheek in the region of the genal angle and the genal spine at its base

are decidedly flattened and have oval rather than circular cross-sections. 2. The anterior border in front of the preglabellar furrow is narrower (sag. and exs.). 3. The triangular area of the fixed cheek determined by the anterior branch of the facial suture, the forward limit of the eye ridge, and the short section of the border furrow running from the facial suture to the anterior pit is larger. 4. In *C. whittingtoni* the palpebral lobe is similar to that in *C. pleurexanthemus* var. *montyensis* and much smaller and lower than in *C. pleurexanthemus*. 5. The lateral expansion of the glabella from rear to front tends to be less and the longitudinal convexity of the part of the glabella in front of the occipital furrow tends to be greater, although both of these are somewhat variable features.

Muscle marks on the cranidium are discussed in a separate section below.

Free cheek.—1. The ocular platform is relatively flatter and lacks the strongly inflated area adjacent to the visual surface of the eye. 2. The border of the free cheek is decidedly flattened, without the semicircular cross-section of *C. pleurexanthemus* var. *montyensis*. 3. The border furrow is shallower and wider.

The plate figures show that, in the first and third features mentioned, there is a tendency in some specimens to vary in the direction of the condition in *C. pleurexanthemus* var. *montyensis*. The area at the base of the eye is never inflated, however, and the typical condition is that of the cheek illustrated in pl. 6, fig. 13.

Rostrum.—Whittington (1941) had not recognized the rostrum of *C. whittingtoni* in the silicified material with which he was working. It has now been found and is here illustrated by a typical example (pl. 6, fig. 22). 1. It is similar to that of *C. pleurexanthemus* var. *montyensis* but its width (tr.) is greater in proportion to its length (sag.), the ratio being about 10:1.2. The curvature of the hypostomal suture tends to be stronger than in *C. pleurexanthemus* var. *montyensis*, although the degree of this arcuation varies.

Hypostome.—1. The single, constantly present, distinctive characteristic is the absence of clearly developed maculae in *C. whittingtoni* and their presence in *C. pleurexanthemus* var. *montyensis*. 2. The hypostomes of the two forms show considerable variation, especially in the longitudinal and transverse convexity of the middle body. However, in *C. whittingtoni* the middle body is, on the average, more inflated than in *C. pleurexanthemus* var. *montyensis*. 3. Again on the average, the posterolateral borders of the hypostome tend to be less strongly convergent posteriorly. The plate figures show adequately the degree of variation and the overlapping in these features.

Thorax.—No distinguishable differences have been observed in the thoracic segments of any of the three forms here considered.

Pygidium.—It is in the pygidium that the most striking differences appear. 1. The posterior margin between the bases of the great spines in most specimens approximates an arc of a circle with center at the midline in the articulating half-ring. This margin is most frequently a smooth curve, although it may show slight prominences marking the ends of some or all of the pleurae of the second to fourth pygidial segments. The broad curvature of this margin gives the typical pygidium a semielliptical outline, rather than the strongly subtriangular one in *C. pleurexanthemus* var. *montyensis*. In some of these respects the pygidium of *C. whittingtoni* comes closer to *C. pleurexanthemus* itself than to the variety. However, the prominences in the margin, representing the second and third segments, are noticeably less strongly developed in most specimens of *C. whittingtoni*. 2. The base of the great spine on the first pygidial segment is broad and flattened so as to have an elongate oval, rather than circular cross-section. 3. The great spines emerge in about the same plane as the central part of the pygidium and then curve very gently upward. 4. In a view perpendicular to the plane of the great spines, the spines are longer and less arcuate than in *C. pleurexanthemus* var. *montyensis*. 5. The border of the pygidium, where it rolls under to form the doublure beneath the pleurae of the pygidial segments, is narrower (in a vertical direction) and the great spines, thus, seem to originate closer to the ventral margin. This is best seen in posterior and lateral views of the pygidia.

Ornament.—A further distinction is the

surface ornament which consists, in *C. whittingtoni*, of a sparser and more uneven covering of granules and small tubercles than in *C. pleurexanthemus* var. *montyensis*.

Many of these distinctions are not readily apparent in young specimens and so these may be more readily confused than adults. But some critical differences appear early enough in the ontogenies so that the two forms may be distinguished at quite small size. The most suitable criterion for distinguishing young cranidia is the cross-section of the genal spine near its base. This exhibits its characteristic shape in cranidia with midlength as small as 1.3 mm. The inflated area adjacent to the visual surface of the free cheek is discernible in specimens fitting a cranidium of *C. pleurexanthemus* var. *montyensis* of 1.0 mm. sagittal length. Hypostomes of *C. pleurexanthemus* var. *montyensis* with a midlength of 0.8 mm. show distinct maculae. Transitory pygidia as early as Degree 7 or 8 can be distinguished on the basis of the vertical angle of the great spines.

MUSCLE MARKS

In addition to the appendifers located in the glabellar furrows, the three forms considered here show other structures which I interpret as attachment points for cephalic muscles. These are situated in two areas: 1) on the glabella itself, and 2) along the preglabellar furrow in front of the median half of the glabella. They are schematically indicated in text-figure 1 which also suggests their variable development.

Muscle marks on the glabella.—A number of pits on the exterior surface of the glabella are believed to indicate points of muscle attachment. These are not equally developed in all specimens, but, from a study of the three forms of *Ceraurus* under consideration here, it seems that, fundamentally, there were seven larger pits and a variable number of smaller ones.

The larger pits are distributed as follows: a pair on the frontal lobe near the preglabellar furrow, a single median pit somewhat behind these but still on the anterior half of the frontal lobe and making with the first pair a broad-based triangle, a pair approximately in transverse line with the third glabellar furrows, and a pair in similar position with respect to the second glabellar furrows. The symmetry with which the pits are arranged does not equal in perfection that exhibited by the glabellar outlines as a whole, but this general pattern of arrangement is apparent. Their relative size, depth, and more exact spacing vary from specimen to specimen. In the silicified specimens of *C. pleurexanthemus* var. *montyensis* and *C. whittingtoni*, most of the seven larger pits are usually visible. In some cases they are deeply impressed, in others they appear as gentle, localized depressions, and in still others some (or rarely all) are wanting. The extent to which the pits are developed does not seem to be related to their position, except that, in general, the posterior pair is more frequently developed in *C. whittingtoni* than in *C. pleurexanthemus* var. *montyensis*. However, this pair is not always present in the former, and has been observed in a few specimens of the latter.

The smaller pits are confined to the triangular area delimited by the anterior triplet of larger pits and the area between this triangle and the preglabellar furrow. They do not seem to be arranged according to any definite pattern whatever, varying greatly in number (0 to about 20) and position as well as in size from specimen to specimen.

On the inner surface of the exoskeleton, evidences of the pits are consistently less marked than on the outer surfaces. The seven larger ones may show as rounded elevations, but only in those cases in which they are deep externally. Interior indications of the smaller pits have not been observed.

It is not known to what extent these pits occur in other species of *Ceraurus*, but they should be looked for. Too little is known of them as yet to estimate their taxonomic value and exact morphologic significance. Prominent median pits on the frontal lobe of the trilobite glabella have been recognized in the family Encrinuridae and in *Heliomeroides* Evitt of the family Cheiruridae. In *Chasmops odini* Eichwald of the family Phacopidae, Öpik (1937) has considered a symmetrical arrangement of a number of pits on the glabella (somewhat similar to arrangement in these species of *Ceraurus*) to represent the points of attachment of muscles supporting the anterior portion of the digestive tract.

Attachments in the preglabellar furrow.—When coated with ammonium chloride or magnesium oxide a number of small areas in the preglabellar furrow are differentiated whose interpretation as points of muscle attachments also seems appropriate. These are very gentle depressions in the floor of the preglabellar furrow and do not attain the aspect of pits as do the areas on the glabella itself discussed above. The two largest of these are located in line with the lateral limits of about the median half of the glabella. This is where the preglabellar furrow shows a slight bend as seen in anterior view (pl. 5, figs. 12, 13). In *Ceraurus whittingtoni* these two areas make slight incursions on the glabella itself (fig. 1c); in *C. pleurexanthemus* (fig. 1a; pl. 5, fig. 6) the preglabellar furrow is slightly wider here. In *C. pleurexanthemus* var. *montyensis* they are less distinct. Between these areas, three (in *C. pleurexanthemus* var. *montyensis* and *C. whittingtoni*) or five (in *C. pleurexanthemus*) smaller areas of similar nature appear. As with the pits on the glabella, so here the symmetry of the arrangement of these areas is not perfect, although one appears to be median with the others arranged in pairs astride the plane of symmetry.

The indications of these areas are so delicate that they can be seen only in the best preserved calcareous specimens and in some silicified ones. In some specimens, they show on the interior as slightly raised areas on the ridge representing the preglabellar furrow. The perfection of preservation required for their observation limits their potentialities as features to be used in defining taxonomic units.

It may be that the median furrow on the frontal lobe of the glabella seen in *Pliomera* Angelin and fainter structures of similar sort in some other genera of the Cheiruridae are greater developments of the median one of these areas, but this is speculation only.

Preservation of muscle marks.—Unlike the appendifers, which served as points of insertion for the muscles operating the appendages, and which are developed as marked projections on the interior surface corresponding to deep impressions on the exterior surface, the pits on the glabella and the areas in the preglabellar furrow here discussed are rather more subtly developed. With excellent preservation they may be readily distinguished on the exterior surface of the exoskeleton, but on all those specimens which I have examined they are less obvious on the interior surface and the smaller ones may not be discernible at all. To interpret such structures, which are more conspicuously developed on the exterior than on the interior, as marking points of muscle attachment may at first seem illogical. However, it is true that when a trilobite cast off his old covering, the muscles within were already present as his new, hard exoskeleton developed through the calcification of his temporarily soft exterior. It is readily conceivable that the exact manner and extent to which calcification proceeded may have been influenced by the presence of subjacent muscles. Before the new exoskeleton became rigid, the muscles may have caused slight depressions in the exterior surface which were then preserved by the final hardening, while the corresponding slight elevations on the interior may have lost their relief as the calcification proceeded inward.

DISCUSSION OF TAXONOMIC DIFFERENCES

In speaking of the ubiquitous occurrence of *Ceraurus pleurexanthemus*, Raymond and Barton (1913, p. 533) remark that it "occurs in the Black River and Trenton at almost all localities where these formations are exposed." The species has been reported from New York to Tennessee and as far west as Minnesota. This has been a broadly conceived species to which have been referred many Middle Ordovician specimens which have the typical features of the genus, *Ceraurus*, and which show general similarities to the type species, but which, upon closer examination, may well represent readily distinguishable species or varieties. Thus, the wide geographic and long geologic range attributed to the species, *C. pleurexanthemus*, is probably more nomenclatorial than biologic.

From the section on systematic paleontology it will be seen that the features which distinguish the two species and one variety considered here have to do primarily with distal parts of the exoskeleton, i.e. the border, the great spines of the pygidium and the elevated eye lobes. In dealing with

silicified specimens etched completely free of matrix these areas are as open to ready scrutiny as any others. However, in the case of calcareous specimens as usually preserved these are just the areas which are most likely either to be covered up by partly enclosing matrix or to be lost or damaged as a result of natural weathering or during collection and preparation. When these critical areas are considered, *Ceraurus pleurexanthemus* var. *montyensis*, n. var., and *C. whittingtoni*, n. sp., stand clearly apart from *C. pleurexanthemus* Green. However, if only the axial region of the exoskeleton is examined, there seem to be no contrasting features on which to soundly base a distinction.

If the strata near Chazy, New York, which have yielded the specimens of the new variety are truly contemporaneous with the strata from which have come the type specimen of *C. pleurexanthemus* and the Trenton Falls specimens upon which the concept of the species has been based, then we may be dealing with two geographic subspecies of a single genus in the strict biological sense, one living to the southwest and the other to the east of Adirondackia, an estimated shoreline distance of 150–200 miles apart. With our present dating means exact contemporaneity cannot be proved and I choose to consider the form from near Chazy as a variety of *C. pleurexanthemus*.

THE ONTOGENY OF *Ceraurus*

Whittington (1941) was the first to describe the ontogeny of *Ceraurus*, based on the species, *C. whittingtoni* Evitt, n. sp. My observations on the ontogeny of *C. pleurexanthemus* var. *montyensis* Evitt, n. var., are in complete agreement with his findings. The remarks which follow present some supplementary information on the ontogeny of *Ceraurus* derived from an examination of a large number of transitory pygidia of the new variety. They concern: 1) axial versus pleural indications of new segments, 2) varying rates of segment development, 3) evidence for multiple moults in one meraspid degree, and 4) certain quantitative data and the conclusions drawn from them.

Quantity of material examined.—The silicified material from Clinton County which was sorted in connection with this study yielded a total of 234 well preserved transitory pygidia of the new variety. These were distributed as shown in the following tabulation:

Degree 5 and lower	— 0 specimens
Degree 6	— 2 specimens
Degree 7	—82 specimens
Degree 8	—91 specimens
Degree 9	—31 specimens
Degree 10	—28 specimens

In addition, 19 of the smallest holaspid pygidia were included in the study. The degree number refers to the number of free segments in the thorax. When dealing with disassociated exoskeletal parts the number of free thoracic segments cannot be observed directly. However, since it is known that there are 11 segments in the adult thorax of *C. pleurexanthemus*, the degree number is calculated as 11, less the number of thoracic segments-to-be which are still anchylosed to form the transitory pygidium. These are the segments lying anterior to the first segment of what will become the holaspid pygidium. In *Ceraurus* the first true pygidial segment is easily recognized, for it is the one bearing the great pygidial spines.

There are several factors involved in the great variation in the numbers of specimens of the different degrees which were found. The decrease in numbers of recovered specimens in stages later than Degree 8 is probably the result of infant mortality. It may be assumed that trilobites were no more blessed than better-known animals of comparable station on the scale of organic complexity and that a large number of offspring were produced in order to insure that a few individuals would reach maturity and continue to propagate the race. The decrease in number of specimens toward lower degree numbers requires a different explanation. This may result simply through the chance that younger stages were not found, or it may reflect a lack of preservable exoskeletons at earlier stages. Should the latter explanation be the true one, its proof must await the gathering of further evidence. Whatever the explanations, these are the facts of the distribution as determined in this case.

Axial versus pleural indications of new segments.—At the close of his discussion of the development of the transitory pygidium of *Illaenus*, Troedsson (1924, p. 224) states

that "the segments appear first in the rachis [axis, of this paper], later on they develop also laterally." In contrast, Stubblefield (1926, p. 365) notes that in the ontogeny of *Shumardia pusilla* (Sars) "incipient lateral division" of a segment may be apparent before there is evidence of a new segment in the axis of the transitory pygidium.

In *Ceraurus pleurexanthemus* var. *montyensis* the pleural portions of the last thoracic segment developed considerably later than the axial ring of the same segment. Thus, in transitory pygidia of Degree 7 (pl. 7, figs. 21, 22, 25, 26) this segment, which is the fourth one from the front, is represented by a well-developed axial ring, but by pleural spines which are so diminutive as to be visible only in ventral view, showing as minute projections behind the pleural spines of the third segment. This suggests the same sort of differential growth in the pleural and axial regions as observed in *Illaenus*. Nothing definitive can be told about the times of appearance of the pleural and axial portions of the true pygidial segments, for all these are already visibly developed in the youngest specimens found. Silicified specimens of young stages of many other genera now under study (also, Whittington and Evitt, in press) suggest that axial and pleural indications of new segments may appear simultaneously, or either one earlier than the other. There seems to be no uniformity among trilobites in this respect and this would explain the contrary evidence of *Illaenus* and *Shumardia*.

Varying rates of segment development.—The development of *C. pleurexanthemus* var. *montyensis* shows that, whatever the relative time of appearance of the axial and pleural portions of a segment, the lateral portions of all segments do not develop with equal rapidity (in this genus at least). That is, the degree of development attained by the segments is not in constant ratio to the length of time which they have been present in the transitory pygidium. If this ratio were constant, there should be a gradual decrease in the extent of the development of the pleurae from front to rear. This holds only if the true thoracic segments alone are considered, but not if the segment which is to become the last segment of the adult thorax is compared with the one next behind it, which is to be the anterior segment of the holaspid pygidium. While the pleurae of the former are still diminutive, those of the latter are already markedly developed into the great pygidial spines. The pleurae of the last thoracic segment are the least developed, but those of the next segment or two to the front are also incomplete. At the same time, and despite their much more posterior position, the short pleural projections of the second, third, and fourth true pygidial segments are already appreciably developed in comparison with the last thoracic segment.

From these observations it is concluded that there is a certain retarding of the development of the pleural portion of the pos-

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EXPLANATION OF PLATE 7

Ceraurus pleurexanthemus Green, Locality 1, Trenton Falls, N. Y.

FIGS. *1, 2*—Hypostome, MCZ 5098, exterior and right lateral views, ×4. (p. 35)

C. pleurexanthemus var. *montyensis* Evitt, n. var., Locality 3.

FIGS. *3, 5, 9*—Hypostome. *3*, oblique detail showing maculae, ×10; *5*, exterior view, ×4; *9*, left lateral view, ×4. (p. 38)

6, 10—Hypostome, exterior and left lateral views, ×5.5. (p. 38)

7, 11—Hypostome, exterior and left lateral views, ×5. (p. 38)

8, 12—Hypostome, exterior view and posterior profile, ×5.5. (p. 38)

C. whittingtoni Evitt, n. sp. Locality 2.

FIGS. *4, 13, 17*—Hypostome. *4*, oblique detail showing maculae, ×10; *13*, posterior profile, ×3.5; *17*, exterior view, ×3.5. (p. 39)

14, 18—Hypostome, left lateral and exterior views, ×3.5. (p. 39)

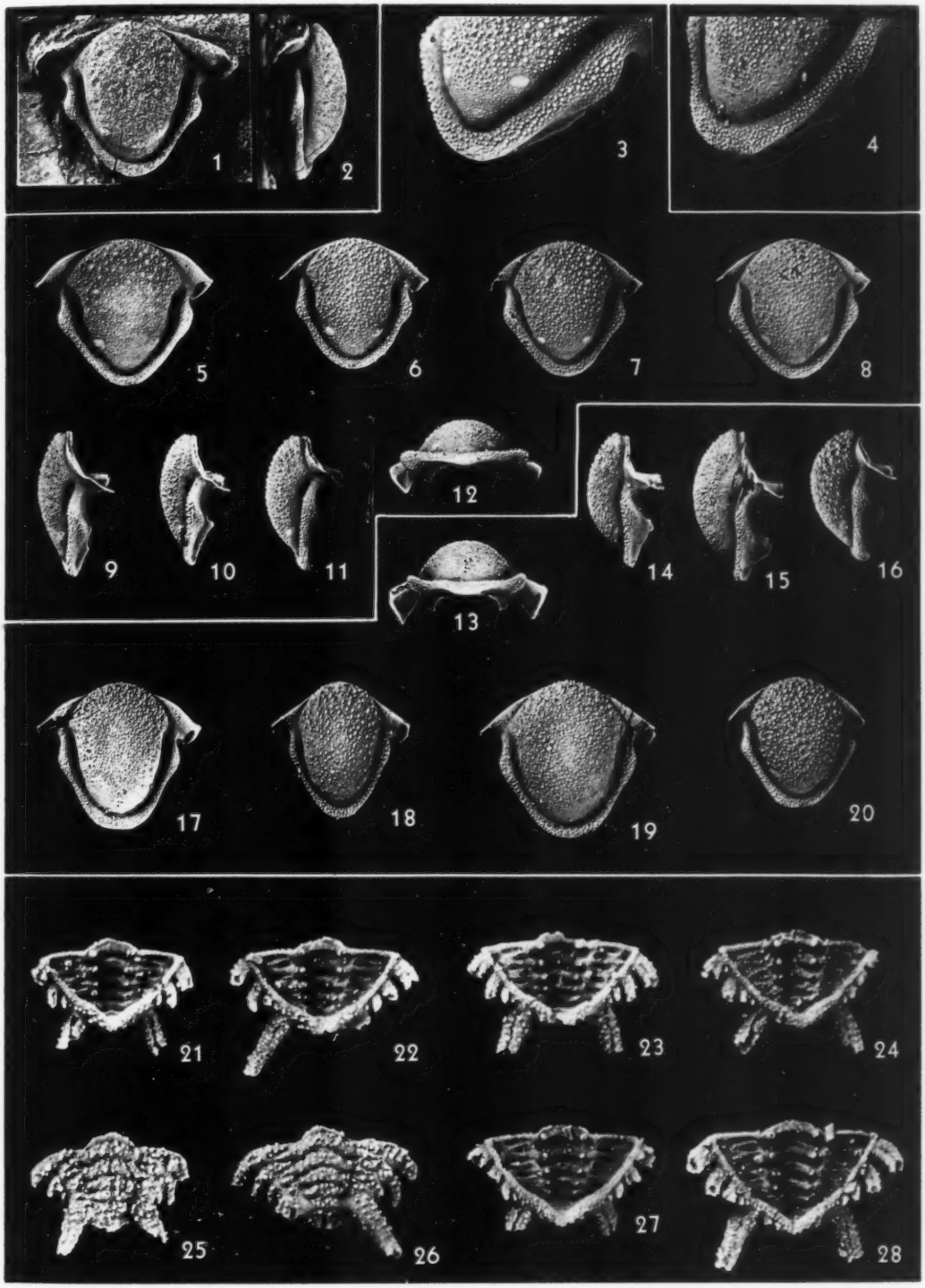
15, 19—Hypostome, left lateral and exterior views, ×4. (p. 39)

16, 20—Hypostome, left lateral and exterior views, ×5. (p. 39)

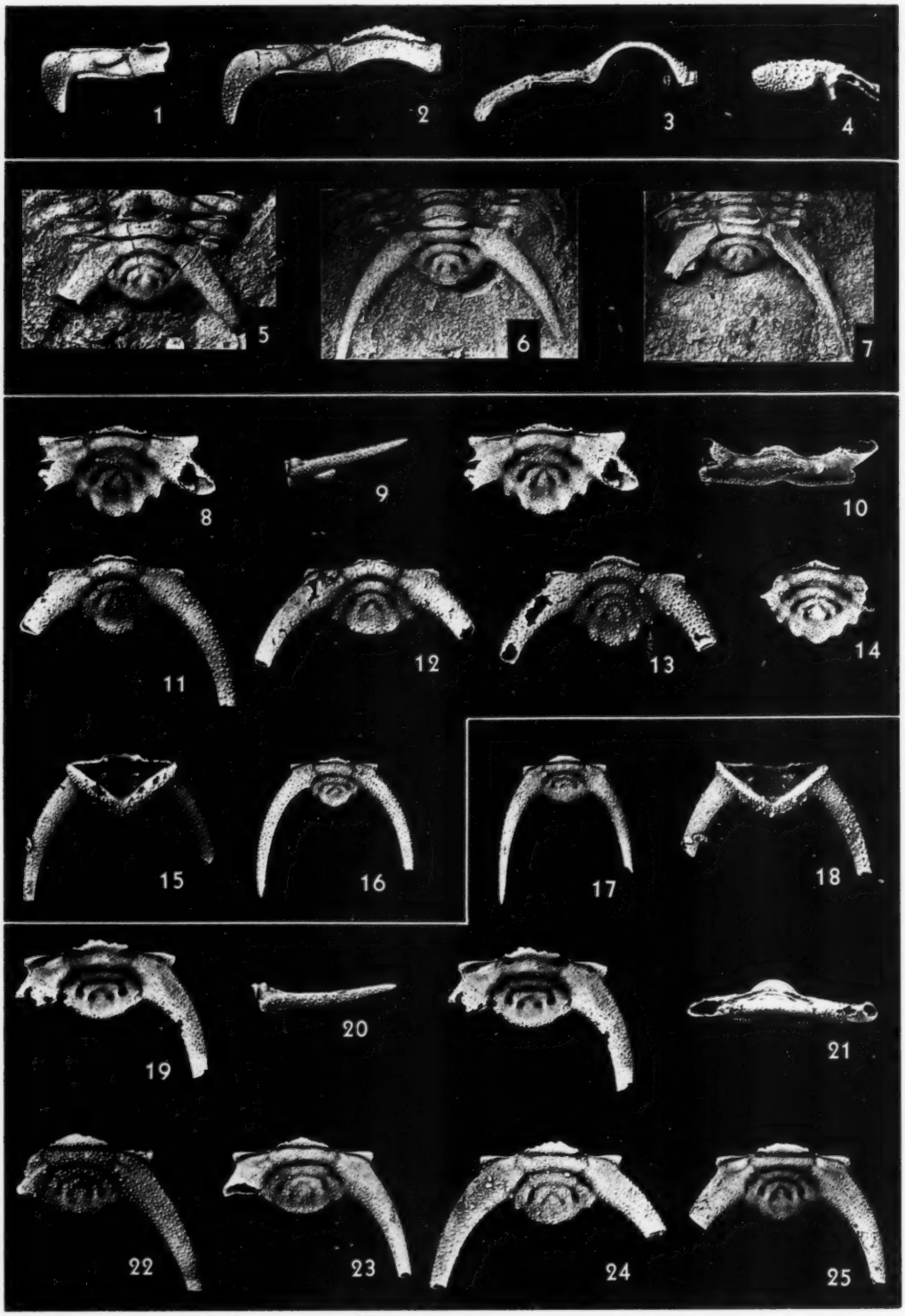
C. pleurexanthemus var. *montyensis* Evitt, n. var., Locality 3.

FIGS. *21–28*—Six transitory pygidia, showing different stages in the development of the posterior thoracic segment and over-all size within a single meraspid degree (Degree 7). *21* & *25*, ventral and dorsal views; *22* & *26*, ventral and dorsal views; *23, 24, 27, 28*, four specimens in ventral view; all ×20. (p. 38)

Note—Figs. *1* and *2*, a calcareous specimen, all others silicified.



Evitt, Ordovician trilobite *Ceraurus*



Evitt and Whittington, *Flexicalymene*

terior thoracic segment, with the last segment the most affected. These features are shown by the specimens of meraspid Degree 7 (pl. 7, figs. 21–28).

If one were to assume that segments exhibit a degree of development proportional to the time they have been present, one might conclude that the case of *C. pleurexanthemus* var. *montyensis* furnishes evidence for a "budding center" for new segments in front of the anterior segment of the true pygidium, for, beginning at the front, there is a progressive decrease in the extent of development of the pleurae as the true pygidium is approached, then a sudden increase when the segments of the true pygidium itself are considered, suggesting that the latter have been present longer. Such an interpretation would bear some similarity to the views of Richter (1912) that new segments from the "budding center" moved forward to the thorax and backward to the pygidium except that in the present case the segments in question are all anchylosed one to another. However, the evidence from many sources points so overwhelmingly to the location of the "budding center" near the posterior extremity of the trilobite body that this explanation cannot be admitted. An interpretation of retarded development of the pleural portions of the posterior thoracic segments explains the case satisfactorily and is in harmony with the principles of segment development in trilobites as generally understood.

Multiple moults within one meraspid degree.—Evidence presented by Barrande (1952) in the case of *Sao hirsuta* Barrande, and by Stubblefield (1926) in the case of *Shumardia pusilla* (Sars) demonstrates clearly that more than one moulting occurred within one meraspid degree. This is the conclusion drawn from the finding of specimens of the same meraspid degree (i.e., with the same number of free thoracic segments) which show progressive change in size accompanied by an increase in the number of segments in the transitory pygidium.

As noted earlier, in the youngest transitory pygidia of *Ceraurus pleurexanthemus* var. *montyensis* which have been found, all the pygidial segments are already present. Thus, the number of these segments is constant during later development and gives no indication of multiple moults. However, specimens of meraspid Degree 7 provide evidence of another sort for multiple moults within one degree.

Under the preceding heading the discussion concerned different degrees of de-

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EXPLANATION OF PLATE 8

Ceraurus pleurexanthemus var. *montyensis* Evitt, n. var. Locality 3.

FIG. *1*—Fragmentary thoracic segment, dorsal view, ×5. (p. 38)

2–4—Fragmentary thoracic segment. *2* & *3*, dorsal and posterior views; ×6; *4*, detail of tip of pleural spine, showing perforations, ×10. (p. 38)

C. pleurexanthemus Green, Locality 1.

FIGS. *5–7*—Three pygidia to show variation in posterior margin between great spines. *5*, MCZ 1, ×3; *6*, MCZ 2, ×2.5; *7*, MCZ 3, ×2. These specimens were the basis for text figures 1–3, respectively, of Raymond and Barton (1913). (p. 35)

C. pleurexanthemus var. *montyensis* Evitt, n. var. Locality 3.

FIGS. *8*, *10*—Pygidium, the holotype, USNM 116693-a, dorsal stereograph and posterior views, ×3.5. (p. 38)

9, *16*—Pygidium, left lateral view and view perpendicular to plane of great spines, ×4. (p. 38)

11, *14*—Four pygidia, showing variation in posterior margin; *11*, ×7; *12*, ×7; *13*, ×6.5; *14*, ×3.5. (p. 38)

15—Pygidium, ventral view, ×8. (p. 38)

C. whittingtoni Evitt, n. sp. Locality 2.

FIGS. *17*, *20*—Pygidium, view perpendicular to plane of great spines and left lateral view, ×4. (p. 39)

18—Pygidium, ventral view, ×8. (p. 39)

19, *21*—Pygidium, the holotype, USNM 116692-a, dorsal stereograph and posterior views, ×3.5. (p. 39)

22–25—Four pygidia, showing variation in posterior margin; *22*, ×5.5; *23*, ×3; *24*, ×5; *25*, ×5. (p. 39)

Note—Figs. *5–7* are calcareous specimens, all others silicified.

velopment of the several segments observable in one specimen. The following deals with variation in the development of the same segment when many different specimens are compared.

If all the specimens of Degree 7 are considered, there is seen to be an appreciable variation in the extent to which the development of the pleural spines of particular segments has proceeded. This is best observed in the case of the last segment of the adult thorax. The more anterior segments exhibit a similar progressive development, but the changes in them are less easily detected. The variations in segment development are shown in the six specimens of Degree 7 illustrated in pl. 7, figs. 21–28. Hand in hand with this goes a variation in the over-all size of the transitory pygidium.

Two possible explanations for these variations among specimens of one meraspid degree may be hypothesized: 1) differential growth among many individuals, or, 2) multiple moults within the one degree. In the case of the first explanation, one would expect that, although the total size of the transitory pygidium varied, the relative size of one feature compared to another would remain constant. This does not agree with the observed condition. Rather there is a relative, as well as an absolute increase in the size of the pleural spines of the last thoracic segment. In the specimens shown on plate 7 the transitory pygidium shows an increase in length of only about 25% from the smallest to the largest, while the ratio of the basal diameter of the pleural spine of the fourth (last thoracic) segment relative to that of the first segment increases about 300%. This rules out the first hypothesis and leads to the conclusion that the observed variation results from several steps in organic development within one meraspid degree accomplished in a succession of moults.

If a greater number of specimens of Degree 6 transitory pygidia had been found, similar changes should have been equally discernible in them. One might expect the same changes to be demonstrable in the higher meraspid degrees of which numerous specimens were available. This is not easily done, however, for, by the time the next degree is reached (Degree 8) the pleural spines of the last segment of the adult thorax have already reached such size that small changes in them relative to the spines of the preceding segments are not obvious.

Quantitative data.—The 253 young pygidia were measured and the following measurements and ratio plotted against the number of specimens for each degree:

1. Total length of transitory pygidium.
2. Length of that portion destined to become the holaspid pygidium.
3. Width of anterior segment of transitory pygidium.
4. Width of anterior segment of that portion destined to become the holaspid pygidium.
5. The ratio of item 2 to item 1.

Measurements were made as accurately as possible. For several reasons this was difficult. The specimens are of small size, the portions to be measured lie at varying inclinations and are of variable convexity, and the preservation of the critical margins is not always perfect. Thus, it was impossible to assure that all specimens were identically oriented and that in all cases exactly comparable portions were measured. Nevertheless it is felt that the data, and the conclusions drawn from them, are sufficiently reliable to warrant discussion.

In all cases the plots of the data for the pygidia of Degrees 7 and 8 fall in compact clusters with no evidence of more than one concentration. The plots for the other degrees are less compact and the distribution is not so regular. This is no doubt due in part to the inferior number of specimens of these degrees. Nevertheless the compactness of the plots definitely decreases with increasing degree numbers. With regard to all single features (e.g. total length) there is some overlapping between degrees (i.e., the longest specimen of Degree 7 is longer than the shortest specimen of Degree 8), but the value of the center of concentration of plots for successive degrees increases in magnitude with increasing degree number (i.e., the mean length of Degree 7 pygidia is less than the mean length of Degree 8 ones).

The conclusions to be reached from these data seem rather obvious and unsurprising:

1. The over-all size of the transitory pygidium increases with successive degrees.
2. The size of the portion destined to be-

come the holaspid pygidium increases with successive degrees.

3. In the more advanced degrees there is greater variation in the magnitude of the dimensions considered than occurs in the earlier degrees. This is probably the result of a more prolonged exposure to environmental factors on the part of the older individuals.

4. The plots of these data do not contribute any confirmatory evidence to the suggestion of multiple moults made in the preceding section. This might have been looked for in the form of more than one concentration of points in the plot of each feature in a given degree. The lack of supporting evidence from this quarter is not considered to be of consequence, however, firstly, because of the crudeness of the measure employed compared with the gradual changes encountered, and secondly, because the over-all size variation within one degree due to the effect of environmental factors (e.g. food supply, etc.) may well mask what might otherwise appear as concentrations about more than one center in the plots. It is conceivable that the over-all size of one individual could decrease (due to some temporarily unfavorable condition, such as curtailed food supply) concomitant with an organic advancement to a higher degree, such as is known to occur among some living arthropods.

At first glance, it may seem that the first two conclusions could be taken for granted. Therefore, I would like to emphasize them, because they are at variance with the condition found in a genus quite similar to *Ceraurus* (a new genus to be described by B. N. Cooper) and represented by two species whose ontogenies have been studied by Whittington and Evitt (reported in a paper to be published by the Geological Society of America). In these two species the over-all size of the transitory pygidium gradually decreases as segments are lost to the thorax one by one, whereas the portion destined to be the holaspid pygidium steadily increases in size. These observations with regard to ontogeny in the new genus are based on a smaller number of specimens than examined in connection with the present study, but they are considered to be sound. Indeed, the investigation of the transitory pygidia of *Ceraurus pleurexanthemus* var. *montyensis* was inspired by a desire to compare them with the growth patterns of the related genus mentioned above. A similar reduction in the size of the transitory pygidium was found by Stubblefield (1926) in specimens of *Shumardia pusilla* (Sars).

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NOTE

In the plate explanations, museum numbers are cited only in the cases of holotypes and the calcareous specimens of *Ceraurus pleurexanthemus*. The other figured silicified specimens are deposited in the U. S. National Museum and are numbered as follows:

C. pleurexanthemus var. *montyensis:* 116693-b to -z.

C. whittingtoni: 116692-b to -z.

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THE EXOSKELETON OF *FLEXICALYMENE* (TRILOBITA)

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ABSTRACT—This paper presents the results of a study of specimens of the Ordovician trilobites *Flexicalymene senaria* (Conrad) and *F. meeki* (Foerste). The rostrum is described on the basis of isolated silicified specimens. It is unusual in not being a flat plate, but sharply flexed along a transverse line. Serial sections of an enrolled calcareous specimen preserving the hypostome confirm that the wing process on the anterior wing of the hypostome rests in a concavity on the anterior slope of the anterior pit of the cranidium. Abundant perforations, interpreted as the loci of sensory hairs and occurring in many sizes, constitute an important feature of the microstructure of the exoskeletons of these species. They are concentrated on those areas which are most apt to come into contact with other objects in the environment. The larger ones are associated with tubercles of the surface ornament, but smaller ones are distributed without regard to such elevations. The type of preservation strongly influences the abundance, size, and distribution of the perforations appearing in any particular specimen. This limits their potential value for taxonomic purposes.

INTRODUCTION

RECORDED occurrences of the genus *Flexicalymene* Shirley, 1936, in North America include many specimens referred to the three species *F. senaria* (Conrad, 1841) of Trentonian age and *F. granulosa* (Foerste, 1909) and *F. meeki* (Foerste, 1910, and varieties) of Cincinnatian age. Indeed, enrolled specimens from the vicinity of Cincinnati constitute one of the most familiar examples of trilobites in general. Reference of a specimen to one species or another of the genus has been to a certain extent dependent upon the known age of the strata yielding the specimen or upon such features as the presence or absence of rib furrows on the pygidial pleurae. It is likely, therefore, that these specific categories are broadly conceived and that further examination of forms referred to them might lead to the distinction of additional species. This condition results in part from an apparent conservatism in the development of the exoskeletal structure typical of the family Calymenidae, so that features have been seized upon and used as the basis of even generic distinctions which might be considered of lesser significance in some other trilobite families (see Shirley, 1936).

In the light of the above remarks it is felt that the discussion which follows does not merely add to our knowledge of the two species on which the evidence is based, but also, by extrapolation, can be safely considered to contribute to the understanding of the exoskeletal design typical of most members of this family of trilobites. The discussion touches upon three items: 1) the rostrum, 2) the hypostome and its relationship to adjoining skeletal parts, and 3) perforations and canals in the exoskeleton.

The basis for this study consists of silicified specimens of *Flexicalymene senaria* from rocks of Trentonian age near Staunton and Harrisonburg, Virginia, and near Chazy, New York, and calcareous specimens of *F. meeki* from near Cincinnati, Ohio. The specimens are in the collections of the Museum of Comparative Zoölogy, Harvard University, and those of the University of Rochester.

THE ROSTRUM

Although many calymenids are preserved as entire specimens and the larger parts of the exoskeleton have been examined in detail, little attention has been directed to the rostrum despite the fact that part of this plate is frequently visible in such specimens. Further information on its structure comes from completely isolated examples etched from Middle Ordovician limestones of the Appalachian region. These silicified rostra have been discovered since the discussion of *Flexicalymene senaria* by Whittington (1941).

The anterior branches of the facial suture

cross the upper surface of the anterior border while running more or less directly forward from the eyes. As they turn downward onto the steep anterior slope of the border they curve toward the midline for a short distance, and join the extremities of the rostral suture. From here the connective sutures run inwards and backwards across the outermost, forward- and downward-facing part of the border. On the doublure, which is flexed abruptly upwards to face downward and backward, the connective sutures bend to run back and slightly outwards (pl. 9, figs. 1–6). The rostral suture is strongly arcuate, running between the broadly V-shaped junctures of the facial and connective sutures in a generally transverse direction across the outer part of the border. The hypostomal suture, which forms the posterior boundary of the rostrum, is also arcuate and shorter than the rostral suture.

The rostrum thus isolated is unusual in that it consists of two distinct portions at an angle to each other. The outer, larger part is here regarded as part of the anterior border, the other as part of the doublure of the cephalon. The surface ornament of each part is distinct. The larger portion bears granules and tubercles (some perforated, see below) in common with the rest of the cephalic border. The smaller portion is smooth and unornamented, like the doublure of the free cheeks. The boundary between these portions coincides with the line of flexure of the rostrum and in some cases it is marked by a distinct ridge (pl. 9, fig. 11).

The thickness of the exoskeleton in the region of the rostrum is quite appreciable so that the smooth sutural edges have noticeable area. The shell material forming the doublure is considerably thinner than that forming the border. The surfaces of the rostral and connective suture meet the inner and outer surfaces of the exoskeleton at large angles, although not always perpendicular to them, but the surface of the hypostomal suture in many cases is very oblique, forming a beveled sutural edge on the posterior margin of the rostrum (pl. 9, figs. 2, 4–6), which matches a similar edge of the hypostome (pl. 9, fig. 9).

In *Flexicalymene senaria* the rostrum changes little in form during the later meraspid period of ontogeny. It becomes proportionally wider transversely and shorter, and less strongly arcuate. The exact proportions and degree of arcuation of the rostral and hypostomal sutures show considerable variation at all stages.

THE HYPOSTOME

Whittington (1941) described the hypostome of *F. senaria* and discussed the relationship of the dorsally projecting "stout, rounded boss" (herein called "wing process") on the anterior wing of the hypostome (pl. 9, fig. 8) to the boss representing the anterior pit in the axial furrow of the cranidium (pl. 9, fig. 7). He concluded that these two points were in contact and, in combination with the hypostomal suture, supported the hypostome against the rest of the cephalon. He also concluded that there was an articulation at these two points, which made possible a rocking movement of the hypostome about them.

A study of the hypostomes and cephalic sutures in a large number of trilobites represented by silicified specimens has convinced us (Whittington and Evitt, in press) that it is unlikely that such movement of the hypostome was possible. The development of anterior pits and corresponding wing processes on the anterior wings of the hypostome is interpreted as a mechanism for support but not articulation of the hypostome.

In an attempt to determine whether or not the interpretation based on the silicified specimens could be confirmed, several calcareous, enrolled specimens of *Flexicalymene senaria* were cut longitudinally. In some there was no trace of the hypostome. In one specimen, whose interior had been partially filled with mud but mainly by crystalline calcite, the hypostome was present. Serial sections of this specimen were ground at 0.1 to 0.5 mm. intervals from somewhat to the right of the midline toward the left, to within a short distance of the left axial furrow. A photograph of each section was made under alcohol and drawings prepared from the photographs. These drawings are presented here as figure 1 and three of the sections illustrated in plate 10, figures 2–4.

The following is a summary of the principal features shown by the drawings and photographs. Section 3 is near the tip of the

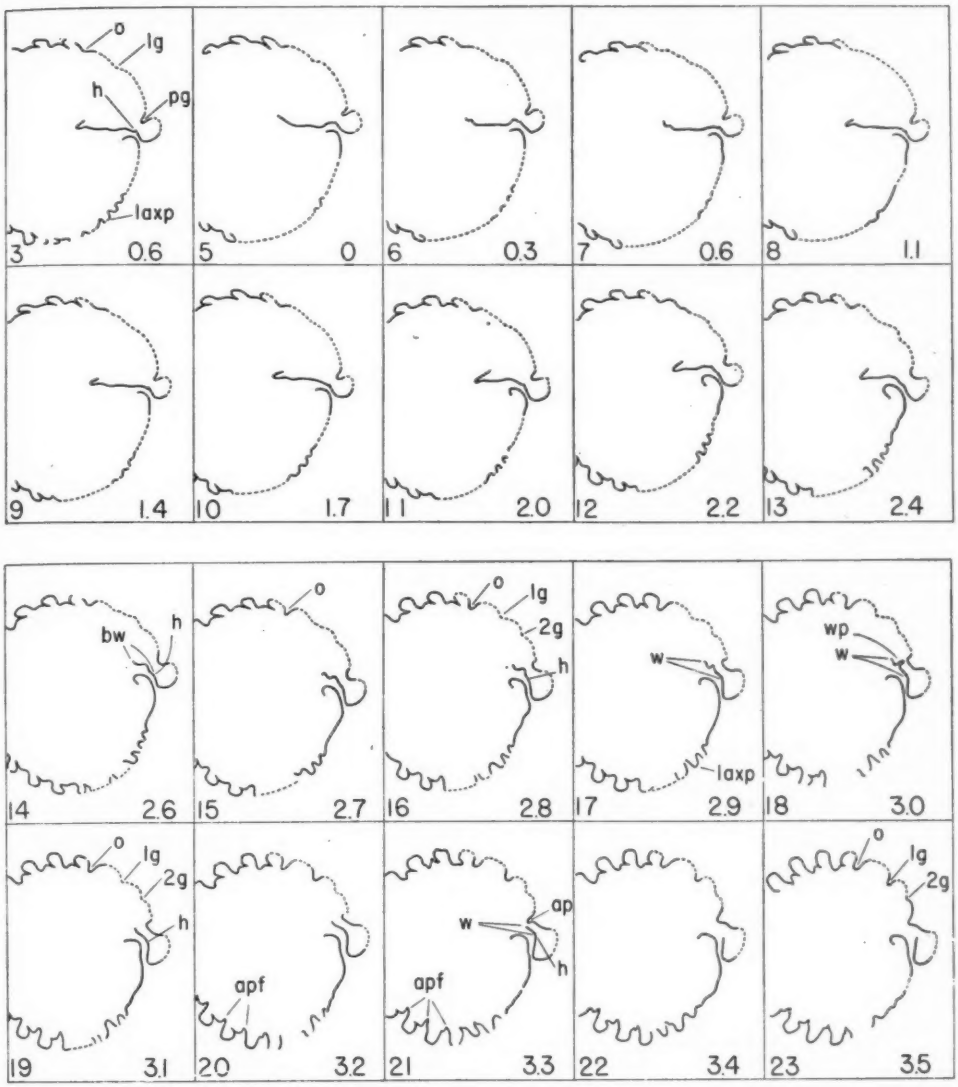


FIG. *1*—*Flexicalymene meeki* (Foerste, 1910) from the Cincinnatian of the Cincinnati area, Ohio; MCZ 5096. Drawings of serial sections through an enrolled individual. Section number at lower left, distance in millimeters from midline at lower right. Section 3 is to the right of the midline, section 5 on the midline, and sections 6–23 to the left. Only the exoskeleton as seen in the section is shown in solid black lines; dotted lines indicate either an internal mold or a generalized margin of the specimen where the exoskeleton has been abraded. ×4/3.

ap—anterior pit, apf—appendifer, laxp—first axial ring of pygidium, bw—base of anterior wing on hypostome, 1g, 2g—first and second glabellar furrows, h—hypostomal suture, w—anterior wing of hypostome, wp—wing process.

right prong of the fork in the posterior border of the hypostome and section 8 is at the tip of the left prong. Intervening sections 5 and 7 show the sharp dorsal flexure of the border in the crotch of the fork and the absence of a doublure in this region. Section 5 is on the midline. The deepening of the glabellar, occipital, and ring furrows as the axial furrow is approached is shown by the contrast between sections 5 and 23.

Section 14 is to the left of the left lateral border of the hypostome and the base (bw) of the anterior wing is seen. In section 18 the wing process (wp) on the anterior wing (w) is shown at its maximum development. Then there is an interval of 0.3 mm. before section 21 shows the anterior pit (ap) at its maximum depth. This interval may result in part from the slight displacement of the hypostome evidenced at the hypostomal suture in sections 3–13, and in part from the fact that the wing process lies against the inner, anterior slope of the anterior pit, and not against its deepest part. If a drawing of section 18 is laid over one of section 21 and a comparison made in transmitted light, it is seen that the tip of the wing process contacts the anterior side of the anterior pit. Section 21 shows that this side of the anterior pit is concave ventrally (cf. pl. 9, fig. 7). This is the position inferred from silicified specimens; i.e. the tip of the wing process rests in the depression on the anterior slope of the anterior pit.

The sections (e.g. section 5; pl. 10, fig. 2) show clearly the turned-down anterior border of the hypostome (cf. pl. 9, figs. 8, 9). This feature sets the hypostome of *Flexicalymene* apart from that of many other trilobites and seems to be associated with raising the main body of the hypostome so as to be out of the way of the posterior extremity of the pygidium upon enrollment. A similar development of the hypostoma is known in the family Harpidae (Evitt, 1951).

The anterior margin of the hypostome, beveled by the oblique hypostomal suture is shown in plate 9, figure 9. In the silicified specimens of *F. senaria* the hypostomal suture extends a short distance beyond the connective suture onto the doublure of the free cheek (pl. 9, fig. 2).

EXPLANATION OF PLATE 9

Flexicalymene senaria (Conrad)

FIGS. *1, 2, 7*—A complete cephalon, silicified. *1*, anterior view, ×3.5; *2*, oblique interior view, showing hypostomal suture on rostrum and free cheeks, ×5; *7*, stereograph of the interior, showing the boss representing the right anterior pit and the excavation on its inner anterior slope for the wing process of the hypostome, ×7.5. Locality 1. (p. 52)

3–5—Rostrum, silicified. *3*, exterior view perpendicular to border surface; *4*, view perpendicular to doublure surface; *5*, oblique view showing angle between border and doublure portions and the sutural edges; ×5. Locality 1. (p. 50)

6—Rostrum, silicified, interior view perpendicular to border surface, ×6. Locality 1. (p. 50)

8, 10—Hypostome, silicified. *8*, oblique stereograph showing wing process on anterior wing and reflexed anterior border; *10*, exterior view, ×8. Locality 1. (p. 50)

9—Hypostome, silicified, right lateral view, ×6. Locality 2. (p. 52)

11—Rostrum, silicified, exterior view showing junction of border and doublure portions, ×6. Locality 1. (p. 50)

12—Rostrum, incompletely silicified, showing the canals which are preserved as pillars joining the two siliceous lamellae representing the inner and outer surfaces of the rostrum, ×10. Locality 3. (p. 54)

13—Anterior border of cranidium, incompletely silicified. The lamella representing the exterior surface has been broken away revealing the canals which are preserved as hollow, spine-like structures projecting from the inner lamella. ×10. Locality 3. (p. 54)

14—Interior surface of glabella, silicified, showing crater-like openings of larger canals, ×10. Locality 3. (p. 53)

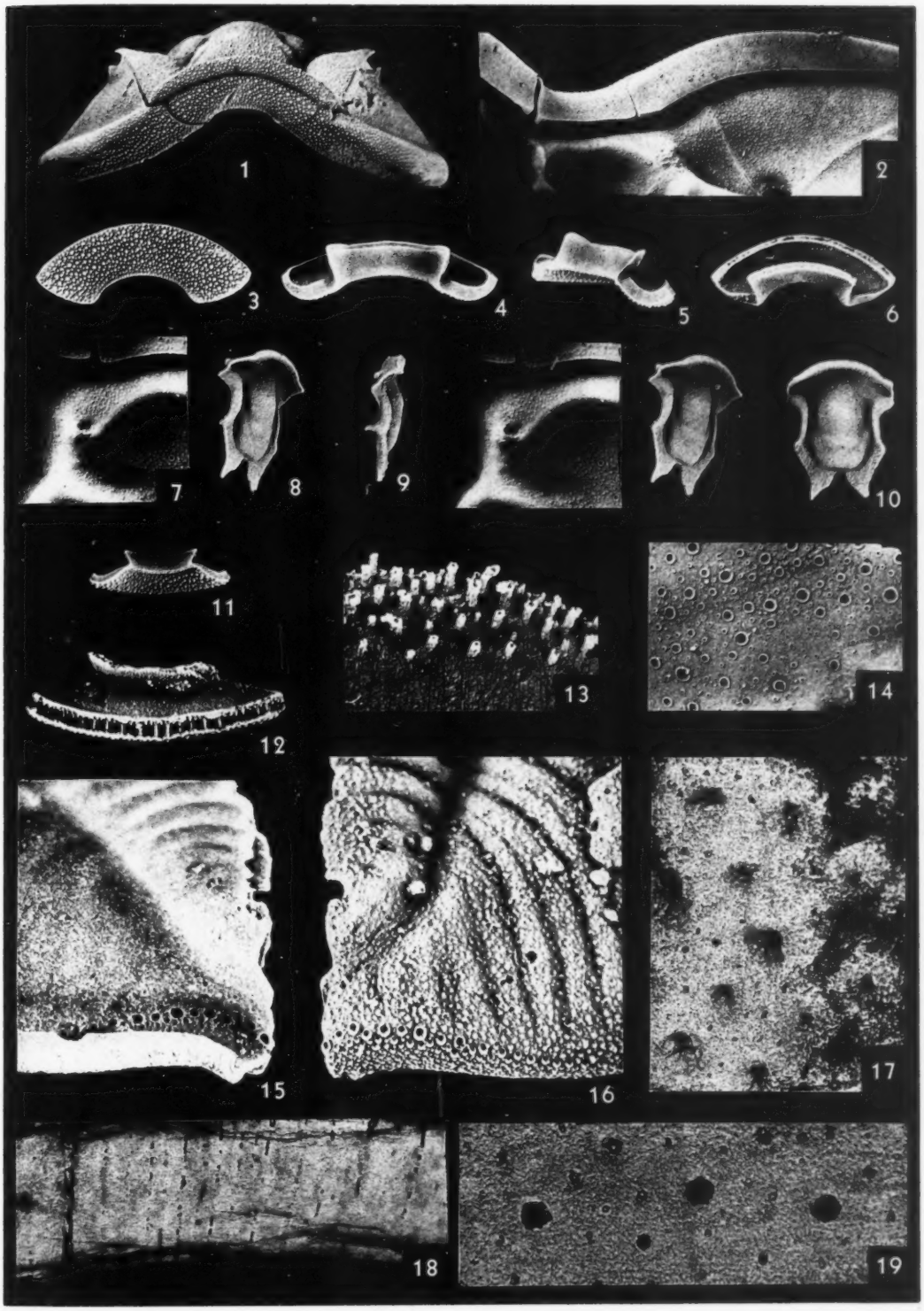
15, 16—Pygidium, silicified (MCZ 5094). Interior and exterior views of the border at the posterior extremity, showing large canal openings. The specimen is broken longitudinally along the midline. ×9. Collected and prepared by P. E. Raymond, 1919; locality 3. (p. 54)

Flexicalymene meeki (Foerste)

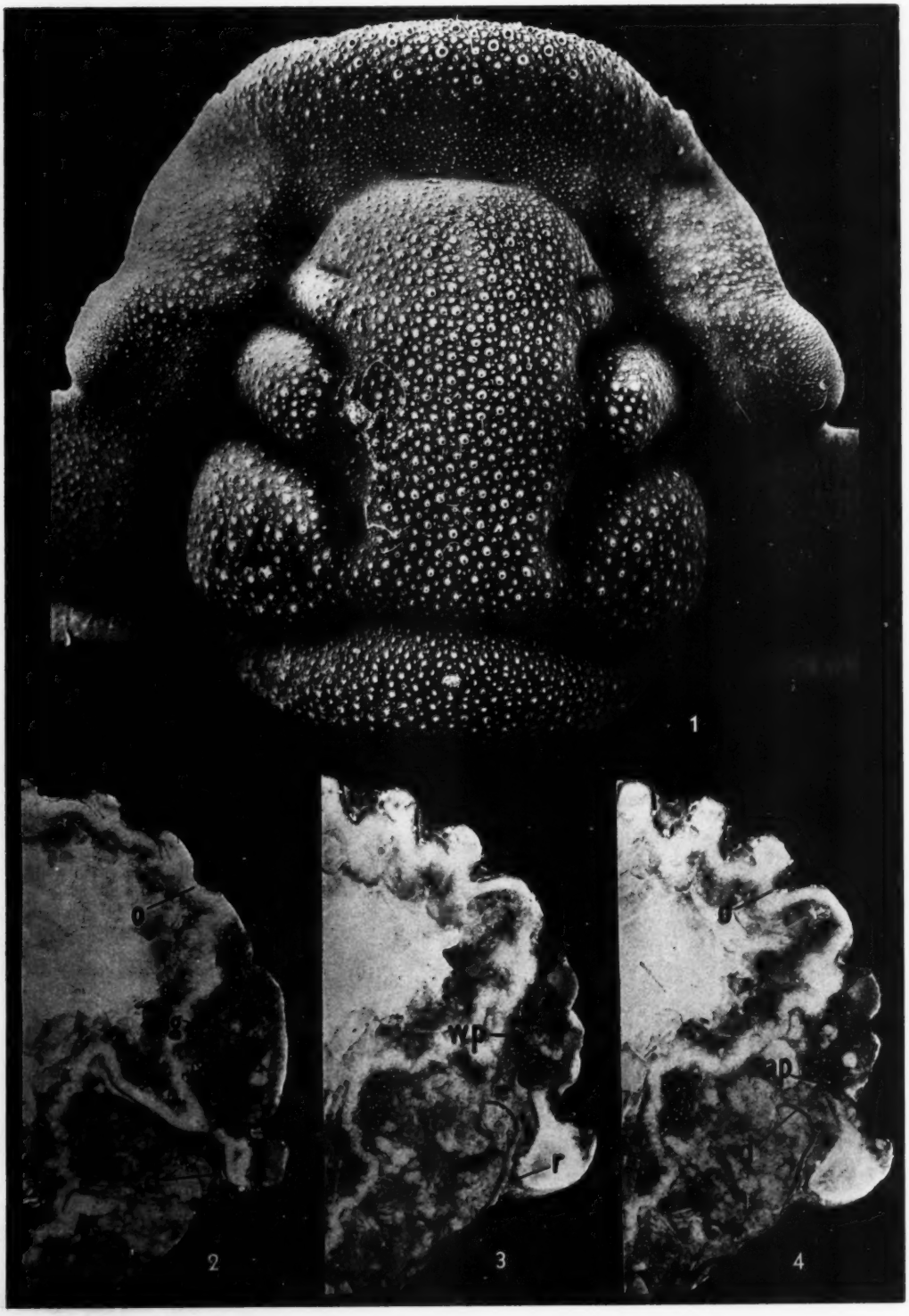
FIG. *17*—Border of free cheek, calcareous. Thin section showing canals (black) filled with pyrite. In the right hand portion of the photo, the section is tangential to the surface, showing two truncated tubercles as light areas with centrally located canals. To the left are similar large canals which emerged upon tubercles, with smaller canals scattered among them. ×70. Locality 4. (p. 53)

18—Border of free cheek, calcareous. Canals partly filled with pyrite, shown in longitudinal section. ×70. Locality 4. (p. 54)

19—Border of pygidium, calcareous. Canals shown in cross-section; larger ones filled with pyrite, smaller ones without. ×70. Locality 4. (p. 54)



Evitt and Whittington, *Flexicalymene*



Evitt and Whittington, *Flexicalymene*

PERFORATIONS

Canals or perforations through the exoskeleton of calymenids were first referred to by Shirley (1936). Their presence in *Flexicalymene senaria* was noted by Whittington (1941). Subsequent investigations have shown us that similar perforations occur commonly in many trilobites, frequently associated with the short spines or tubercles of the surface ornament. So far as we know, they seem to be lacking in forms with a smooth surface. These openings are interpreted as the loci of sensory hairs which had their bases in the soft tissue beneath the exoskeletal cover and which, by penetrating it, gave a certain tactile sense to the outer surface. Well preserved calcareous specimens of *Flexicalymene meeki* have been studied in external aspect and in thin sections prepared from various portions of the exoskeleton. Silicified specimens of *F. senaria* showing the perforations also have been examined. These studies give additional information on the size and form, the distribution, and the manner of preservation of the perforations.

Size and form.—In the species of *Flexicalymene* examined, the perforations range in size from 0.0004 mm. to 0.075 mm. in diameter. The smallest ones can be seen only in thin sections of the best preserved specimens under high magnification, while the largest are discernible with the naked eye. The smaller perforations are cylindrical for their total length, but many of the larger ones increase in diameter as they approach the inner surface of the exoskeleton so that their openings on this surface are crater-like in form with distinctly elevated rims (pl. 9, fig. 14). The canals are straight or nearly straight. Their axes of length may be perpendicular to the surfaces of the exoskeleton or quite oblique to them in some areas.

Distribution.—Shirley (1936, p. 414) remarks that in a specimen of *Calymene lata* examined by him the canal openings are situated on tubercles on the exterior surface and are "not on the highest point, but a little way down that side which would be away from the current when the trilobite moved forward." This is only a partially accurate generalization when applied to the canals in the specimens we have seen. The larger canals seem to be typically associated with tubercles on the surface. Many of them do emerge on the slopes of these tubercles, but many others emerge at their summits, especially on the border (pl. 10, fig. 1) or where the tubercles are situated on a portion of the surface with a posterior slope. In contrast to the large canals, those of smaller diameter are located without regard to the surface elevations. Their openings may occur around the large apertures on the crests or slopes of tubercles or in the depressions between adjacent granules and tubercles (pl. 9, fig. 17). Possibly these smaller canals escaped Shirley's notice because of unfavorable preservation, and his statement referred to the larger ones only.

When different portions of the exoskeletal surface are considered, the distribution of the canals is seen to be uneven. They may be closely or widely spaced, and the relative numbers of openings of different diameter vary greatly. The concentrations are greatest on those areas which are most likely to come into contact with other objects in, and inhabitants of, the environment. The largest perforations (suggesting the longest and stoutest tactile hairs) are located on the anterior border of the cranidium, the border

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EXPLANATION OF PLATE 10

FIG. *1*—*Flexicalymene senaria* (Conrad). Silicified cranidium (MCZ 5094) in exterior view, showing canal openings located on tubercles of the surface ornament, ×9. Collected and prepared by P. E. Raymond, 1919; locality 3. (p. 54)

2–4—*Flexicalymene meeki* (Foerste). Serial sections of an enrolled calcareous specimen, the interior filled with crystalline calcite and argillaceous material. ap—anterior pit of cranidium; d—doublure of pygidium; h—hypostome; g—glabella; o—occipital furrow; r—rostrum wp—wing process on anterior wing of hypostome. *2*, section no. 5, along midline; *3*, section no. 18, showing wing process of hypostome at its maximum development; *4*, section no. 21, showing anterior pit of cranidium at its maximum development. ×4. Locality 4. See page 50 and text figure *1*. (p. 52)

portion of the rostrum, and the posterior extremity of the pygidium (pl. 9, figs. 15, 16). Next in order of size, and first in order of concentration of numbers of perforations of all sizes, is the glabella, followed by the axial rings of the thorax and pygidium. The lateral borders of the free and fixed cheeks, the extremities of the thoracic pleurae, and the borders of the pygidium are also well supplied. The density is low on the flatter surfaces of the pleural lobes (the free and fixed cheeks within the border furrows and the thoracic and pygidial pleurae), although even in these parts the density is locally higher and a few large perforations may occur in regions of abrupt increase in surface convexity, such as at the brinks of the pleural furrows of the thorax and pygidium and at the fulcra of the thoracic pleurae. An exception to this generalization seems to be the palpebral lobe (in our specimens of *F. senaria* at least). Although this is certainly an exposed prominence, perforations of large size seem to be entirely lacking here (pl. 10, fig. 1). A single canal of large diameter emerges from the apex of the genal angle on the fixed cheek. Some portions of the surface, especially the bases of the deeper furrows, are devoid of perforations.

Preservation.—All the specimens at hand demonstrate the presence of these canals and perforations, but the different types of preservation emphasize different aspects of their structure and cause them to produce quite different effects. Their courses through the skeletal material can best be studied in calcareous specimens where the canals have been filled with a contrasting substance. In such specimens even the smallest canals may be visible. However, details concerning the apertures of the canals on the inner and outer surfaces of the exoskeleton are not so readily discerned. Weathering on the outside may destroy the finer sculpture of the surface, while the inner surface is generally inaccessible. Not all calcareous specimens are equally suitable, for, in the absence of some filling which contrasts with the shell material, a minimum amount of recrystallization would be sufficient to erase all evidence for such minute structures. In silicified specimens, the smallest canals may not be preserved at all, but the inner and outer surface details relating to the apertures of the larger canals can be readily studied.

The most advantageously preserved specimen we have seen is an example of ***Flexicalymene meeki*** from the Cincinnati region. The calcareous exoskeleton is light brown in color and translucent. The canals have been filled with deposits of pyrite (grains of which are also common in the matrix) and stand in sharp contrast to their surroundings when viewed under xylol or alcohol. Other specimens collected from the same area show a variation in the degree to which the pyrite fills the canals. In a specific portion of the exoskeleton all the canals may be incompletely filled (pl. 9, fig. 18), or some may be completely filled, others incompletely filled, and still others empty (pl. 9, fig. 19).

The exoskeletons of the silicified specimens of *F. senaria* from New York and Virginia are preserved as granular silica. We are explaining elsewhere (Whittington and Evitt, in press) why we believe that this preservation is in the form of a replacement. The process by which the exoskeleton was replaced began from the two surfaces and the replacement in many cases did not proceed to completion. Thus, the fossils, when etched from the matrix with hydrochloric acid, consist of two siliceous lamellae (representing the inner and outer surfaces) with a space between. At first glance the surface details appear to be preserved with fidelity, but as regards the canal openings, this is true only where the larger canals occur. The apertures of the larger canals are easily seen on the exterior as perforations situated on tubercles, and on the interior as crater-like openings. The canals themselves are preserved as hollow columns of silica extending between the two lamellae (pl. 9, fig. 12). If the two lamellae are separated, then the canals may show as spine-like projections from the inner surface of one of them (pl. 9, fig. 13). In such instances the oblique angles which some of the canals make with the surface of the exoskeleton can be seen. As for canals of smaller diameter, however, neither the openings for them, nor columns representing them are to be seen. This might be due to their original absence in this species. A check on suitably preserved calcareous specimens has not been possible. More likely it results in part from the blocking of the minute pores by grains of the replacing

silica, thus preventing replacement of the linings of these canals, and in part from the slenderness of such structures as the resulting columns would be (if they were present at one time), and their consequent weakness after the enclosing matrix has been etched away.

Summary.—From this study of perforations in specimens of *Flexicalymene* certain generalizations can be made which should apply to any trilobites in which such canals are present. A considerable variation in the size of the canals is to be expected, with some of very small diameter. The larger ones tend to be associated with granules or tubercles on the exterior surface, but the smaller ones may be distributed without regard for such elevations. In respect to preservation, it would seem that, although canals of all sizes may have been present originally, the apparent presence or absence, the number, size, and distribution of canals in a fossil specimen depend in large measure on the nature of post-depositional processes, which may have varying effects on the microstructure of the exoskeleton without megascopically distinguishable effects. It is to be expected that these processes in some cases will completely destroy all evidence of canals, in others preserve them completely, and in still others selectively emphasize the presence of canals of certain sizes. These facts limit any potential value the canals may have in trilobite taxonomy, although they may constitute an important feature of the microstructure of the exoskeleton.

MANUSCRIPT RECEIVED MARCH 5, 1952

LOCALITIES

The numbered localities referred to in the plate explanations are as follows:

Locality 1—road cut, about 0.3 mile northeast of Greenmount Church, Rockingham County, Virginia; lower Martinsburg formation (Trentonian).

Locality 2—field exposures, about 3 miles north-northeast of Long Glade, Augusta County, Virginia; Trentonian limestones, possibly part of the Martinsburg formation.

Locality 3—loose blocks and outcrops near Little Monty Bay, Chazy, Clinton County, New York; Trentonian limestones.

Locality 4—near Cincinnati, Ohio; Cincinnatian strata.

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, PP. 56–61, 8 TEXT FIGS., JANUARY 1953

SYSTEMATIC POSITION OF THE PELECYPOD *EULOXA*

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ABSTRACT—A thorough study of the shell morphology of *Euloxa* shows that this genus is a veneroid, and its nearest relatives are chionids.

INTRODUCTION

THERE are many examples of monotypic genera and even a few monotypic families in the fossil record. Some of these strange groups are known from only one specimen, but others are known from a number of specimens found in a few localities in a relatively restricted area.

Two explanations may be given for the sudden appearance of these monotypic genera and families. These groups may have developed slowly outside the geographic area where they are now found as fossils and invaded it later when conditions were favorable. The area of origin of the monotypic group may now be inaccessible to collectors; it may be as yet undiscovered; or it may have been destroyed by erosion or some other geologic process. The main weakness of this explanation is that the appearance or disappearance of a monotypic group is not always correlated with a diastem, and the portion of the bed where it is found may show no difference or break in lithology from the portions of the bed above and below. The second explanation is that the monotypic group arose quite suddenly in the area where it is now found as fossil. In my opinion this is probably what happened in most species where there were relatively small numbers of individuals. In order to have migration and expansion of a species, the population or populations making up the species must increase in size; otherwise any considerable amount of migration and expansion of the geographic range of the species is impossible.

As an example of a monotypic group, I have chosen the genus *Euloxa* because it is known from only a few specimens which have been collected on the Rappahannock and James Rivers. This genus has been found only in the upper fossiliferous zone of the St. Marys formation which is considered late Miocene in age by Cooke, Gardner, and Woodring (1943, chart). These pelecypods lived about 20 million years ago, which from the standpoint of geologic time is quite recent. The fauna of the St. Marys formation in Virginia and Maryland has been relatively well collected and studied. There seems to be little reason why this unusual genus is not better known except for the fact that it is rare.

Euloxa was first described by Conrad in 1840 (pp. 40, 41) as *Venus latisulcata*. In 1852 d'Orbigny (p. 112) placed the species in the genus *Astarte*. Conrad (1863a, p. 585) proposed the new genus *Euloxa* for the species *latisulcata*, but still attempted to show its relationship to the venerids by citing it as *E.* (*Venus*) *latisulcata*. In 1872, however, Conrad (pp. 52, 53) gave no indication of family relationship. Dall (1903, p. 1502) placed *Euloxa* in the superfamily Cypricardiacea, family Pleurophoridae. Dall's family Pleurophoridae was really nothing more than another name for "incertae sedis" and contained the following genera: *Trapezium*, *Coralliophaga*, *Orycto-mya*, *Cyclas*, and *Euloxa*. The Pleurophoridae followed the Astartidae in Dall's classification. Lamy (1920, p. 262) briefly mentioned *Euloxa* and claimed that it was a cyprinoid. The latest work on the genus has been done by Gardner (1943, pp. 65, 66), who erected a new family Euloxidae for the genus; and on the basis of morphology, it is a perfectly justified procedure, in my opinion. Gardner placed the family Euloxidae in the superfamily Cyprinacea. The genus *Euloxa* has been considered a venerid, an astartid, a pleurophorid, and finally a cyprinoid. This complete summary of the taxonomic history of *Euloxa* is presented as further proof of the strangeness of the genus.

The main problem of this work, therefore, is to ascertain the relation of *Euloxa* to other pelecypods, and this can be done only by a detailed study of the shell morphology of *Euloxa* and by comparing it with representatives of other pelecypod families.

Harris (1951, pp. 17, 18) has described *Euloxa* sp. from the Ocala limestone of Florida. The material is poorly preserved, but Harris claims that there are four teeth in the hinge of each valve. If this is true, then these specimens cannot belong to the genus *Euloxa*, for the hinge of the genus is entirely different from that of the Ocala specimens.

COMPARATIVE MORPHOLOGY OF *Euloxa*

Size.—*Euloxa* is a relatively small pelecypod. Of the ten specimens examined, the length of a mature shell is about 22 mm., the height about 18 mm., and the convexity of both valves about 14 mm. The largest specimen seen was 24.6 mm. long, 20.5 mm. high, and 14.8 mm. in convexity. Size gives little or no indication of the relationship between *Euloxa* and other pelecypods.

Form of the valves.—The valves are equal and not gaping. The dorsal margin is nearly triangular; the anterior margin is broadly rounded; the ventral margin is straight; and the posterior margin is truncated. This truncated area is marked exteriorly by a well-developed sulcus which makes a depressed area on the posterior fifth of the shell. There is a slight indication of a sulcus on some of the arcticids and chionids. I am using the family Chionidae in the restricted sense that Frizzell (1936, p. 65) used it.

Nature of the shell.—The shell is porcellaneous and somewhat chalky in *Euloxa*. This condition is common in heterodont pelecypods.

Ornamentation of the shell.—The ornamentation of *Euloxa* consists of large, rounded, concentric undulations which are better developed toward the ventral margin. There are concentric riblets superimposed upon the undulations. This type of ribbing is most nearly like that of *Anomalocardia* or *Lirophora*, although it also resembles some of the arcticids and astartids. *Euloxa* has no crenulations on the interior ventral border. This is also true of the arcticids and some of the astartids. Almost all of the chionids have crenulated margins, but some other veneroids consistently do not show this feature. *Euloxa*, like the arcticids, has no lunule and escutcheon, although there are depressed areas in front of and behind the beaks. Nearly all of the chionids, however, have a lunule and escutcheon, as do the astartids.

Position of the beaks and ligamental area.—The beaks are prosogyrate and the ligament opisthodetic. This condition is typical of heterodont pelecypods.

The ligament.—The ligament of *Euloxa* is parivincular and rests on nymphae. This is typical of the condition found in veneroids and arcticids.

The hinge teeth.—The various family relationships have been based primarily on different interpretations of the hinge teeth of *Euloxa*. The hinge of the left valve has three cardinal teeth and is like a chionid hinge in appearance. Tooth 2a is small, narrow, and perpendicular to the ligament. Tooth 2b is large, thick, slightly narrower at the dorsal end, and nearly parallel to the ligament. Tooth 4b is also nearly parallel to the ligament, but it is long, narrow, and slightly curved. The teeth of the right valve are much more difficult to interpret. If the interpretation of the left valve is correct, tooth 3a is absent. Tooth 1 is large, triangular, and perpendicular to the length of the shell. Tooth 3b is narrow, grooved in the middle, and sloping backwards. The large nympha on the right valve gives the appearance of being another tooth parallel to 3b, and it is slightly dorsal and posterior to it. The hinge formula of *Euloxa* is, then,

$$\frac{1,3b}{2a,\ 2b,\ 4b}.$$

It is interesting to compare this formula with those of the Arcticidae, Astartidae, and Veneracea. The hinge of *Arctica* is a well developed one with the formula

$$\frac{\text{AI, AIII, 3a, 1, 3b, PI}}{\text{AII, 2a, 2b, 4b, PII}}.$$

In order to derive the hinge of *Euloxa* from *Arctica* the five lateral teeth and tooth 3a must be eliminated. The occurrence of this great change is very unlikely. The astartid

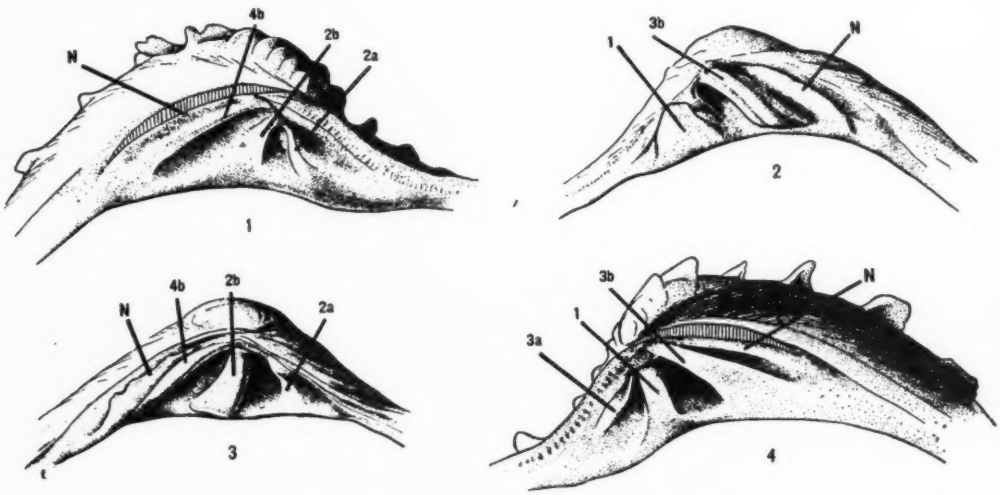
hinge formula is much more variable. Lateral teeth may or may not be present, and the cardinal teeth may be four to six in number. In the astartid species with the same number of teeth as *Euloxa*, the cardinal teeth are not of the same size and shape as those of *Euloxa*. The veneroids vary greatly in number of teeth; nevertheless the chionids consistently lack lateral teeth and have a hinge formula as follows:

$$\frac{\text{3a, 1, 3b}}{\text{2a, 2b, 4b}}.$$

In general, tooth 3a is quite small. The veneroids generally do have a pallial sinus, although most of the chionids have only a small one, and a few have none at all.

DISTRIBUTION OF *Euloxa*

The St. Marys formation has been divided into three zones; the lowest is nearly devoid of fossils, but the two above it are very fossiliferous. Mansfield in Gardner (1943, p. 6) states that *Euloxa latisulcata* occurs in the lower fossiliferous zone at the west end of the Stratford Cliffs on the Potomac River. However, all of the localities listed by Gardner (1943, p. 66) are in the upper fossiliferous zone. I know of no specimens



FIGS. *1–4*—Cardinal teeth, 1, 2a, 2b, 3a, 3b, 4b. Nympha, N. *1*, *4*, *Chione* (*Lirophora*) *paphia* (Linné), Recent; St. Thomas, Virgin Islands; *1*, left valve, *4*, right valve. Hypotypes USNM 530503. *2*, *3*, *Euloxa latisulcata* (Conrad). Miocene, St. Marys formation; Urbanna, Virginia. *2*, left valve, lectoparatype, ANSP 19446, *3*, right valve, lectoholotype, ANSP 19546.

other teeth of *Lirophora* and *Anomalocardia* are similar to those of *Euloxa* in size, shape, and position (text figs. 1–4). The hinge of *Euloxa* apparently lacks tooth 3a and seems to be shortened, but the resemblance of the hinges of *Euloxa* and the chionids is striking.

Adductor muscle scars and pallial line.—The adductor muscle scars of *Euloxa* are approximately equal in size, but the anterior one is deeper and not so rounded as the posterior one. The pallial line is integripalliate, and it has a small indentation at its posterior end. Similarly, the Arcticidae and Astartidae have no pallial sinus. The

from the lower fossiliferous zone and therefore believe that Mansfield was in error.

Euloxa has been reported from Urbanna and near Jones Point on the Rappahannock River, from the Old Claremont Wharf on the James River, and from the west end of the Stratford Cliffs on the Potomac River. I have seen specimens of *Euloxa* from all but the last-named locality. The map (text fig. 5) shows the general area from which the genus has been reported. It is interesting to note that, although the St. Marys formation is well represented in southern Maryland, *Euloxa* has not been found in that state.

CONCLUSIONS

In the discussion on comparative shell morphology of *Euloxa* with the astartids, arcticids, and veneroids, it was noted that *Euloxa* had some morphologic characters in common with all three groups. Undoubtedly the most important evidence is that of the hinge teeth, and in this respect *Euloxa* closely resembles the veneroids, particularly the chionids. The hinge formula of the chionids is

$$\frac{\text{3a, 1, 3b}}{\text{2b, 2a, 4b}}.$$

Tooth 3a is quite small in many of the chionids. In *Euloxa* tooth 3a has completely disappeared (text figs. 1–4). The remaining teeth are of much the same size and shape as those of the chionids, and, furthermore, they occupy about the same position on the hinge plate. In other words, the hinge of *Euloxa* looks like a slightly shortened and modified chionid hinge, just as the latter is a slightly modified and shortened venerid hinge. Thus there is a shortening of the hinge and a decreasing number of teeth from the venerid, through the chionid, to the hinge of *Euloxa*. Other morphologic characters of *Euloxa*, although some are not typically veneroid, are found in this large and variable superfamily. For example, there are some veneroids without a pallial sinus, without crenulations on the inner border, or without radial ribs. The unique morphologic characters of *Euloxa* are the well developed posterior sulcus and the loss of tooth 3a. *Euloxa* appears to be an aberrant branch of the chionids and resembles the genera *Lirophora* and *Anomalocardia*. From the standpoint of evolution it is also much more likely that *Euloxa* is related to a relatively young and rapidly evolving stock like the Chionidae rather than to some small, relatively stable and relict families like the Arcticidae and the

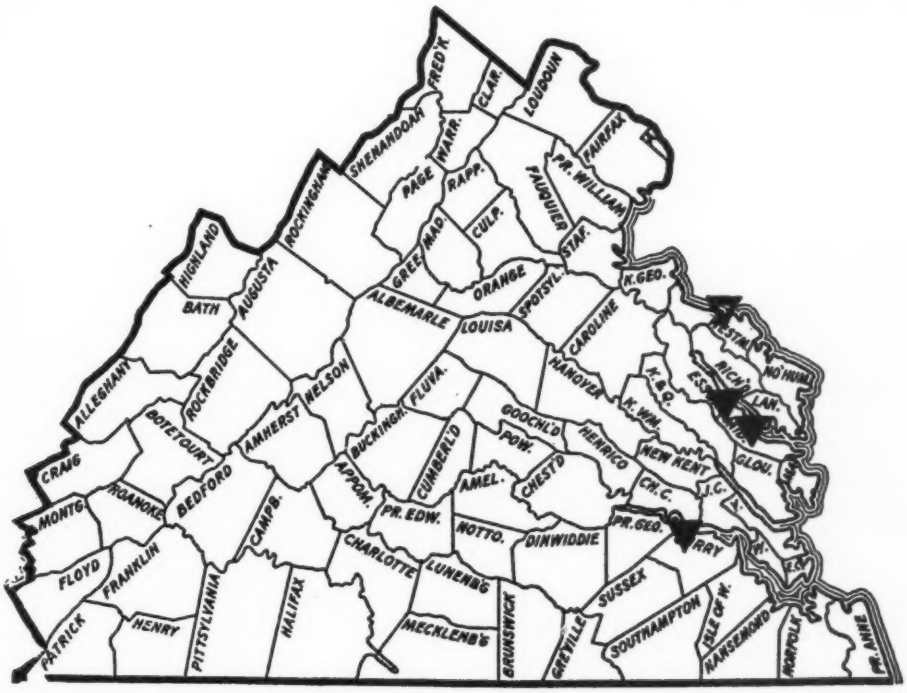


FIG. 5—Map of part of Virginia showing general localities where *Euloxa* has been reported. Solid triangles, specimens examined by me from these localities. Open triangle, specimens reported from this locality in literature.

Astartidae. Conrad was much more nearly correct in his original allocation of the species *latisulcata* to the genus *Venus* than were later workers who placed it in other groups. The systematic position of *Euloxa* can tentatively be shown as follows:

Superfamily Veneracea Menke, 1830
Family Chionidae Frizzell, 1936
Subfamily Chioninae Frizzell, 1936
Subfamily Euloxinae Gardner, 1943
Genus *Euloxa* Conrad, 1863
Euloxa latisulcata (Conrad), 1840

The systematic arrangement I have given may seem somewhat conservative. On the basis of morphology, Gardner (1943, p. 65) is justified in giving the Euloxidae the rank of a family. However, the primary aim of a classification, according to most systematists, is to show phylogenetic relationship. *Euloxa* is obviously a chionid, and in order to show this I have considered the Euloxinae as only a subfamily of the Chionidae.

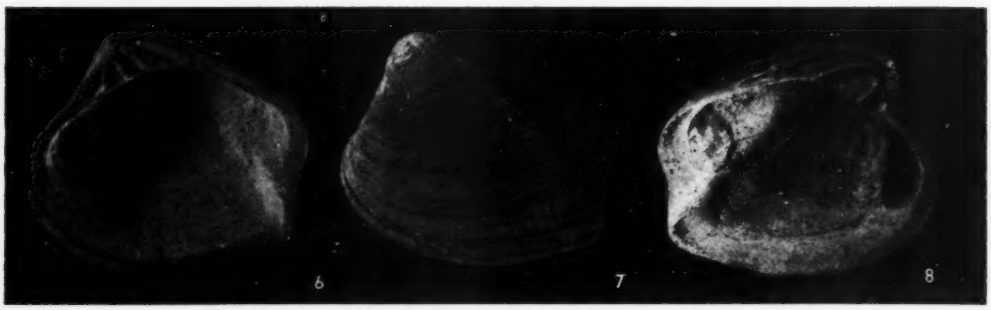
The ancestral species of *Euloxa* is at present unknown. This genus is one of the aberrant and unsuccessful pelecypods which appeared for a short time, was poorly represented in number of species and individuals, and disappeared just as suddenly, leaving no known descendents. Theories of evolution must take into account and explain these aberrant forms which appeared from time to time throughout the paleontologic record.

SPECIMENS OF *Euloxa latisulcata* EXAMINED

Lectoholotype ANSP 19546.
Six lectoparatypes ANSP 19446.
One lectoparatype USNM 561467.
One hypotype USNM 214407.
One specimen in the paleontological collection at The Johns Hopkins University.

ACKNOWLEDGMENTS

I am particularly indebted to Mrs. Sally Lee, who made the drawings of the pelecypod hinge teeth. Dr. A. A. Olsson of the Academy of Natural Sciences of Philadelphia obtained for me the type lot of *Euloxa latisulcata*. Dr. Harold E. Vokes and Mr. Druid Wilson lent me a specimen of *Euloxa* which they located in the paleontological collection at The Johns Hopkins University.



FIGS. *6–8*—*Euloxa latisulcata* (Conrad), ×1.5. *6*, Interior view of right valve of lectoholotype, ANSP 19546, St. Marys formation, Urbanna, Virginia. *7*, Exterior view of left valve of hypotype, USNM 214407, St. Marys formation, Old Claremont Wharf, James River, Virginia. *8*, Interior view of same specimen as fig. *7*.

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AMERICAN TRIASSIC ESTHERIDS

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ABSTRACT—The classification of fossil Conchostraca has been difficult due to their many differences in form, attributed largely to sexual dimorphism, and to variations in shell characteristics, particularly surface sculpture, which demand more accurate discernment for proper taxonomic assignment. Additional diagnostic elements, such as growth zones, carapace volume, and sexual differentiation, are introduced. The well-known generic name, *Estheria*, has had to be abandoned for this crustacean bivalve and is replaced by *Isaura* Joly. The classic Triassic estherids, *Isaura minuta* (Goldfuss) and *Isaura ovata* (Lea), and the relationship between *Estheriella* and *Leaia*, are reexamined on the basis of Lea's type specimen. Seven new species from the Triassic of eastern North America, Venezuela, and Colombia are added.

INTRODUCTION

THE fossil Conchostraca, bivalved crustaceans, represent a widespread group, ranging in age from Devonian to Recent; but their classification has not always been considered to be a thankful task, due to the existence of so many anomalous forms and variations, which may discourage the investigator. One of the first comprehensive books on fossil estherids is that of T. Rupert Jones (1862), whose conservative classification and thorough reports are still a source of valuable information.

MORPHOLOGY

The recent Conchostraca are grouped by Kobayashi and Huzita (1943, p. 162) in five families, based chiefly on the soft part anatomy, although a few differences of carapace characteristics are apparent. The same authors (1943, pp. 263–275) have also made a thorough and important study of the morphological features of living estherids compared with those of fossilized types, and they have come to the conclusion that many of the morphologic characteristics of the carapace lack absolute value for classification.

Another weighty anatomical feature of the Conchostraca is their sexual dimorphism, which expresses itself in the shape and appearance of the fossil carapace. Daday de Deés (1915) shows, in his systematic monograph of the living phyllopodian Conchostraca, sexual distinctions in the carapace in almost all of his species. In the genera *Caenestheria* and *Caenestheriella* 85% of the males are larger than the females, the areal surface difference averaging about 15%, although a few register up to 35%. Twenty-five species figured belonging in *Eocyzicus* and *Cyzicus* show about 88% males larger, averaging 18% surface increase. Not quite half of the male carapaces are more roundly shaped than are those of the females, which tend to have a longitudinal outline. Fisher and Jones, and also Chi (Kobayashi and Huzita, 1942, p. 112) have noted that the carapace in the male is broader than in the female. In their paper the latter authors state that the female type is more common than the other. This is an important observation, as the differences of the sexes may be numerically shown in a type population. There are a number of other minor distinctions noted; but the important points crystallizing out of these various findings are that the male type is the less abundant, larger in size, and tends to have a more roundish shape, while the female is inclined to the more longitudinal form. In spite of these pronounced distinctions, it is hardly possible actually to prove the sexual dimorphism of fossil estherids, and it may be advisable to distinguish two diverging groups as the α-form, showing male characteristics, and the β-form, of the opposite sex. This method should avoid duplication in classification.

The picture of the varying form of the concentric growth-segments, so typical of most of the estherids, also needs some clarification. Basically, the test of most con-

chostracans consists of numerous segments, which are fused to a narrow, slightly outstanding growth-line, or growth ring, the latter being composed of bundles of round channels, apparently providing a vascular system, which supplies the necessary elements for further expansion of the growth segment. Generally, the mature adult carapace gives little information about its growth. However, occasionally some fossil shells which had not completed their growth cycles, reveal that the valves enlarged by adding a new growth zone of closely set growth rings of varying number, whose interspaces gradually expanded until they reached mature dimensions. The peripheral terminal seems to be mostly a growth ring. In other species, particularly those with few growth segments, the expansion occurs by addition of a single segment, growing to nearly full size before others are added.

In general, three growth zones can be distinguished, the umbonal zone, followed by the intermediate zone and finally the terminal, or peripheral, zone. The umbonal zone is recognized as the juvenile phase by the smaller number of segments, pronounced curvature, and its size, which is close to that of immature shells. The intermediate zone is indicated by the larger intervals of the segments, and the terminal zone by closely set, flattening out, growth rings and diminishing intervals, which often do not mature to full size. In some species the different zones do not always follow the outline of the preceding one, and in others the intermediate zone is not always recognizable.

It is not certainly known what time element is involved in the development of these successive growth segments, or growth zones, nor is the life span of the fossil estherids, in general known. However, E. Willard Berry (1926, pp. 429–433) presents an interesting description of a new, living, estherid species, including the morphological development from its nauplius stage to its final development. He states that the life cycle was completed in 23 days. The carapace develops at the third day as a minute spot, showing eight growth lines at the ninth day. Only one segment is added up to the sixteenth day. Berry's study certainly presents some valuable information on the growth of the fossilized forms.

The radial cross section of a segment of a fossil estherid in its most simple form shows a linear, or somewhat curved, interval, joined by the slightly protruding growth lines. Normally, the outline of the exterior surface is curved in concave arcs, forming a nearly cycloidal curve. In some species with thin tests the inside and outside surfaces show an identical reflex pattern. In more robust, well-curved species, such as *Isaura* ("*Estheria, Pseudestheria*") *ovata* (Lea), the interior surface preserves the fundamental convex cycloidal pattern, while the outside face is often altered by reinforcing layers along the margins of the growth lines, mostly obscuring the latter altogether and developing a more sinuous curvature, or terrace-like undulations.

Also anathema for classification are the design patterns displayed on both sides of the growth sections, generally known as reticulation, striation, and granulation. Living estherids, with few exceptions, show such well-imprinted patterns that they cannot but attract the attention of the investigator. The preserved evidence on fossil material is extremely meager, and few men have been fortunate enough to observe them. The often described and intriguing reticulation of *Isaura* ("*Estheria*") *minuta* (Goldfuss) has been shown in an excellent photograph (Gross, 1934), (see pl. 11, fig. 7). The striated and dotted pattern can be more often observed. Kobayashi and Huzita (1943) have made a careful study of the surface pattern on living estherids, comparing the different designs of the main groups. A pattern may be dominant in several genera, but not all of them will have these characteristics. Some patterns may change in different stages of growth. The final conclusion of these authors was that none of the morphologic pattern characteristics are useful for generic identification. Daday de Deés (1915) shows different species of *Caenestheriella*, some having dotted patterns, others linear, dendritic, or reticulate designs. *Caenestheriella donaciformis* Baird (Daday de Deés 1915, p. 180) is shown with different patterns on the male and female shells. *Cyzicus californicus* Packard (ANSP, Crst. Coll. no. 12000) has the same perfect indented mesh pattern as *Isaura minuta* (Goldfuss), connected near the growth lines

by a narrow band of straight bars, while the interior is invested with identically sized polygonal dots. *Howellites colombianus* Bock, n.sp. has striated and dendritic sculpture. These observations only accentuate the finding of the two Japanese authors that surface patterns of the growth segments of fossil estherids cannot form a reliable basis for generic distinction.

Many of these details have to be observed before a valid new genus or species can be established. A type population is necessary to point out the many variations of appearance, sex-type, and growth stages. Species based on a single specimen can hardly be of more than temporary value. The pitfalls of surface sculpture have been already pointed out. The shape and number of growth rings may vary greatly in the same species. However, processes of growth, growth stages, the relationship of the growth rings to the interspaces, their bearing on the shape, thickness and volume of the carapace, and the distinction of sexual dimorphism, may lead to a broadly acceptable classification.

While examining uncounted Mesozoic estherids, two types of carapaces seemed to form morphological and generic variations. The most frequent type is of round-oval to elliptic shape, with moderate to numerous growth lines, broad interspaces, robust, thick shell, with a rather narrow terminal growth zone, but considerable carapace volume and pronounced sexual forms. The second type is of oval to roundish shape, with numerous, more delicate growth lines and varying intervals, thin shell only moderately curved, with a corresponding small carapace volume and a wide terminal growth zone. The difference of the volume of these two types suggests, besides their morphological distinction, a considerable variation of their soft anatomy.

The first group comprises the larger part of the Mesozoic estherids, led by *Isaura minuta* (Goldfuss) and *Isaura ovata* (Lea). The second, so far less frequently found group, is represented by the new genus *Howellites*, particularly *Howellites princetonensis* Bock, n.sp.

PROBLEMS OF SYNONYMY

The fundamental classification of the estherids, living and fossil, has repeatedly been shaken by such unfortunate things as preoccupation, misinterpretation, and incomplete records. Numerous efforts have been made to unravel the mounting complications; but, as in so many time-worn taxonomic wrangles, a clear and true picture is still wanting.

It is generally recognized that the generic name *Estheria* Rüppell, Strauss-Dürchheim, 1837 is the first assignment for this type of crustacean, which is based on the single species *Estheria dahalacensis*. The generic name had, however, been previously employed by Robineau-Desvoidy (1830) for a dipterous insect.

At about the same time Audouin (1837, p. 124) established the genus *Cyzicus* to which he assigned the nomen nudum *Cyzicus bravaisii* and *Limnadia tetracerus* Krynicki, the character of the latter species being already known and being quite different from that of *Estheria dahalacensis*.

In 1842, the French scientist M. N. Joly described a new living estherid, which he called *Isaura cycladoides*. (pp. 293–361).

Daday de Deés (1915, p. 235), dealing with the same synonymy, believed that the new genus *Isaura* Joly, to which Joly had assigned *Isaura tetracerus* Krynicki, *Isaura dahalacensis* Rüppell and *Isaura cycladoides*, n.sp., may be considered a valid successor to preoccupied *Estheria;* but, he felt that *Isaura* was also preoccupied by a genus of hexacorals, *Isaures* (Savigny, 1817).

However, Andovin (1826, p. 229) points out that the type of *Isaures* Savigny (a colloquial name) was never described, and he proposed *Palythoa* as the genus name for this type of coral.

Therefore, the name *Isaura*, as used by Joly, which is also distinguished by two letters from "*Isaures*" (Savigny), is in no way preoccupied and should be the legal replacement for the name *Estheria*. Agassiz's correction (1844) of the French word "*Isaures*" to "*Isaura*" a coelenterate (=*Palythoa* Andovin 1826) appears to be unjustified and does not affect Joly's establishment of *Isaura* in 1841. Raymond (1946, p. 220) questions whether *Isaura* is a properly described genus, either as a coral or as a crustacean. However, the reading of Joly's unsurpassed description of *Isaura cycladoides* (1842) including the genus (p.

341), will quickly dissipate any doubts.

In 1912 (pp. 172, 173) Depéret and Mazeran established the two subgenera, *Euestheria* and *Lioestheria*, one of which is synonymous with *Estheria* (=*Isaura*). (Int. Rules of Zoological Nomenclature, Article 9.) *Euestheria* (true "*Estheria*") is considered to be the direct synonym, judging from the nature of the name. *Lioestheria lallyensis* is the subgenotype.

Two other authors successively proposed to replace the preoccupied genus *Estheria*. Kobayashi and Huzita (1943) suggested the name *Estherites*. In 1946, Raymond proposed the genus *Pseudestheria* for the remainder of the estherids, which were not assigned otherwise. It now appears that both genera were anteceded by *Isaura* Joly, 1841.

Daday de Deés (1915, p. 51) recommended for fossil estherids the genus *Palaeestheria*, which is not valid as it lacks the necessary definition and is preoccupied by *Isaura* Joly. Although the latter did not include fossil species in his genus, these were recognized as members of the genus *Estheria* at that time and their valves are similar.

Marlière (1950) tried to avoid the taxonomic difficulties by demoting the genus *Euestheria* (Raymond) to its previous rank of subgenus. This can hardly be accepted since *Estheria* is a fly.

Raymond (1946) apparently raised the subgenera *Euestheria* (which is preoccupied) and *Lioestheria* to full genera by selecting *Lioestheria lallyensis* as the "genotype." He established the family Lioestheriidae, which included, in his broad description (p. 230) forms with "a carapace with numerous lira, etc." represented by the type *Lioestheria lallyensis*, from which many of the remaining forms of *Isaura* are fundamentally distinct. It is proposed to unite this large group in the now more acceptable family Isauridae.

Family Isauridae Bock, n.fam.

Carapace elliptic, oval to subcircular, having moderate to numerous concentric growth segments of varying size connected by narrow growth lines; surface of test well curved to moderately shaped; radial cross section cycloidal, semicycloidal or undulated; growth zones of varying dimensions distinguishable, indicating phases of growth; inner and outer surface between growth lines smooth or having surface patterns of varying form; radial growth stria extending over exterior surface in rare cases; sexual differentiation indicated in shape and size of carapace.

Genus Isaura Joly 1841

Estheria Rüppell, Strauss-Dürchheim, 1837, non Robineau-Desvoidy (1830).
Isaura Joly, 1841; Joly, 1842, pp. 293–361.
Euestheria Depéret & Mazeran, 1912, pp. 172, 173.
Estherites Kobayashi & Huzita, 1943, pp. 196–202.
Pseudestheria Raymond, 1946, pp. 243–256.
Estheria (*Euestheria*) Marlière, 1950, pp. 24–30.

The above genera are synonymous with *Isaura* Joly for the reasons cited. *Pseudestheria* is further objectionable as it is based on punctation in the intervals, which is not considered to be a sufficient generic distinction (Kobayashi and Huzita, 1943). As Raymond (1946, p. 243) states that "*Pseudestheria* and *Euestheria* are much alike, the difference being entirely in the sculpture," that "*Pseudestheria* must inevitably become a sort of dumping ground for not-too-well preserved fossils," no harm seems to be done by eliminating this genus.

Furthermore, Raymond (1946, p. 225) had already assigned the "punctate form" to *Caenestheriella* Daday de Deés, separating from this genus the new type, *Bairdestheria*, which he distinguishes by its radial markings. However, this generic differentiation can hardly be sustained, as it is based again on surface patterns. Raymond's selected genotype, *Caenestheriella donaciformis* Baird (Daday de Deés, 1915, p. 180, fig. 38, o, p) is shown as having combinations of punctate, reticulate, and linear surface patterns, which also differ between the male and female shell. Furthermore, Raymond included several species in his new genus *Bairdestheria* (pp. 225–230) which either show reticulate surface patterns or mixed patterns, supporting the views of Kobayashi and Huzita (1943) that surface patterns have little generic validity. All fossil species of *Bairdestheria* could be easily grouped with the Lioestheriidae the de-

scription of which also includes forms with radial markings, or with the Isauridae. This also would reserve the family Cyzicidae Stebbing for living estherids, whose distinction is largely based on soft anatomy.

ISAURA OVATA (Lea)
Plate 11, figures 1–4

Posidonia ovata LEA, 1856, p. 77.
Estheria ovata (Lea) JONES, 1863, pp. 94–101.
Pseudestheria ovata (Lea) RAYMOND, 1946, p. 254.
Pseudestheria emmonsi RAYMOND, 1946, p. 253.
Pseudestheria hindei (Jones) RAYMOND, 1946, p. 254.
Pseudestheria pennsylvanica (Wanner) RAYMOND, 1946, p. 255.
Estheria mangaliensis pennsylvanicus WANNER, 1926, p. 25.
Lioestheria inornata RAYMOND, 1946, p. 233.

Introduction.—It is regrettable that Lea gave only an incomplete description of this important Triassic estherid, which was later quite adequately treated by Jones (1862, pp. 84–99). Unfortunately Jones did not refer to the type specimen, but to the estherids found by different investigators from varying horizons of the Newark basin. While Jones conservatively grouped the most of them in Lea's species, others established new ones on slight variations. As *Isaura ovata* is a profuse member of the eastern Triassic fauna, a large collection was secured for this study; but the most fortunate find was the rediscovery of Lea's dusty type specimen. Many specimens of *Isaura minuta* (Goldfuss) were obtained from the Keuper of Germany, so that the relationship of these two outstanding Triassic conchostracans can now be properly defined. The writer had been inclined to group these two species together (Bock, 1946), chiefly persuaded by Jones' details of reticulate patterns and test appearance (Jones 1862, pl. 2, figs. 1–8, 26–38). However, the size of these two species alone, as disclosed by the actual specimens, shows sufficient specific differentiation. Lea's type specimen of *Isaura ovata*, and identical ones from other localities, form the basis of the following account.

Description.—Two forms, apparently sexdimorphic in character, are distinguished. α-form (male). Outline oval to subround; hinge line short, less than half of test length; anterior-posterior margin nearly equally rounded; posterior side slightly broader than anterior one; umbo located dorsal-laterally, near center of hinge line. Growth segments averaging 20 to 32. Length of adult shell 7 mm., width 5.8 mm., ratio 1.2. Rare in comparison to the β-form. β-form (female). Valves oval to elliptical; hinge line straight, about half of valve length; posterior portion well rounded, less broad than anterior side; umbo close to the anterior end in first quarter of hinge line, dorsal-laterally inclined; growth segments 18 to 35. Length of adult shell 7 mm., width 5 mm., ratio 1.4. Identical traits. Three growth zones are distinguishable, the umbonal, the intermediate, and the terminal one, having nearly similar surface areas, but a varying number of growth segments. The average number of consecutive growth segments amounts to 10-6-8 per zone, with the umbonal zone having the largest number, being most convex, and forming the maximum thickness of the carapace of about 2.4 mm. In the intermediate zone the concentric segments broaden to a maximum width of 0.7 mm., the growth line being 0.2 mm. thick. The terminal zone flattens out, with its segments becoming gradually smaller, showing in the marginal region only growth lines and gradually diminishing interspaces.

The cross section of the test resembles a cycloidal curve, convex and well preserved on the internal surface, showing distinct, slightly protruding, growth lines. On the exterior surface growth lines are thickened, obscured, forming undulating or terrace-like ridges which become concave-cycloidal in the terminal zone. Some of the peripheral segments are occasionally invested with fine indistinct radial striae, not apparent on older segments, which may be the cause of a notched or crenated ridge, occasionally formed by single or double-edged growth lines.

The surface pattern of the interspace is in most cases indefinable, probably due to abrasion and the state of preservation. The outside pattern is distinct from that of the interior surface, consisting of six to eight rows of somewhat irregularly placed roundish to polygonal tubercles, about 0.03 mm. wide and high, arranged in the concave interspace between the growth-lines (pl. 11, fig. 4). The interior surface pattern is of similar design and dimensions, however,

imbedded in the convex surface as indentations or pores. Superficially, the sculpture appears to be finely reticulate.

The dimensional formula for different specimens follows.

Type No.	Location	Dimensions Lgth. mm.	Hgt.	Ratio	Growth lines Total No.	Interspace mm. max.	Growth line mm. max.	Hinge line mm.	Sex	Valve Shape	Pattern Surface
Holotype	Phoenixville	7	5	1.4	10-8-6 24	0.5	0.2	4.5	fem. adult	left oval	— outside
Plesiotype	Phoenixville	7	5	1.4	11-8-13 32	0.5	0.2	4.5	fem. adult	right oval	— outside
Plesiotype	Edison	8	6	1.33	7-5-7 19	0.6	0.2	5.0	fem. adult	left oval	Dots outside
Plesiotype	Edison	6	4.5	1.33	9-8-5 22	0.5	0.15	4.5	fem. adult	left oval	Dots outside
Plesiotype	North Wales	7.2	5.1	1.4	11-7-5 23	0.5	0.2	3.5	fem. adult	right oval	Dots outside
Plesiotype	North Wales	7.0	5.8	1.2	11-8-7 26	0.5	0.2	—	male adult	left round	Dots outside
Plesiotype	North Wales	6.5	5.5	1.2	12-8-7 27	0.5	0.2	—	male adult	left round	Holes inside
Plesiotype	North Wales	4.1	3.0	1.4	12-0-0 12	0.2	0.1	2	fem. juvenile	right oval	— outside

Discussion.—It is easily recognized that the distinction of dimorphic types, of inside and outside test characteristics, and of the different growth stages encountered in a type population, must eventually reduce the large number of inflated species. The dimensions of *Isaura ovata* collected from many horizons, discussed by Jones (1863), fall entirely in the realm of Lea's type specimen. Jones' varying version of reticulated, dotted, and linear surface patterns, may be explained by the difference of the sculpture displayed on the inside and outside of the shell. "*Pseudestheria*" *emmonsi* Raymond (1946, p. 253) and "*Estheria*" *mangaliensis pennsylvanicus* Wanner (1926, p. 25) are identical with Lea's species. The latter (fig. 2, right) especially, is not distinguishable from *Isaura ovata* (Lea). "*Pseudestheria*" *pennsylvanicus* should also be eliminated for taxonomic reasons. Variations should not be elevated to the rank of a species without revealing adequate paleontological evidence and new authorship. "*Estheria*" *hindei* Jones (Raymond's "*Pseudestheria*" *hindei*) can be recognized in many populations of *Isaura ovata*. "*Lioestheria*" *inornata* Raymond is merely a broader, single, form with an indistinctly drawn surface appearance, which Jones rightfully assigned to "*Estheria*" *ovata* (1863, pl. 2, figs. 28–30).

Location.—This species is found throughout a narrow belt of the Lockatong formation, about 50 km. long, extending from the Delaware River to Phoenixville, Pennsylvania, and has been found also in a similar belt near York, Pennsylvania. The dark, fine grained Lockatong sediments contain this species in profusion at many places, revealing that these little swift-swimming crustaceans must have led a muddy life in stagnant or slightly moving water in association with *Bairdia* (*Candona*) species and in less happy relations with large *Coelacanth* fishes, whose coprolites often contain abundant remains of their shells. The type specimen, as stated by Lea, was found near Phoenixville, where fresh-water mussels also were frequent. Other locations are at North Wales, near the corner of Welsh and Evans Road, at Miller's Quarry, near Edison, and at Clouster's Quarry, at Tradesville, all in Pennsylvania. The age of the belt is believed to be middle Keuper, particularly of the Schilfsandstein-Bunte Mergel series (Upper Triassic).

Depository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype no. 20010. Plesiotypes nos. 200102–4.

ISAURA MINUTA (Goldfuss)
Plate 11, figures 5–7

Posidonia minuta GOLDFUSS, Petref. Germaniae, 1834–40, p. 118, pl. 113, figure 5a, b.
Estheria minuta Alberti, JONES, 1862, pp. 42–72, pl. 1, figs. 28–30; pl. 2, figs. 1–8; pl. 4, figs. 8–9.
Estheria minuta Goldfuss, PICARD, 1911, p. 619, pl. 23, fig. 2.
Estheria minuta Goldfuss, BOCK, 1946, pp. 8–11, fig. 3.
Euestheria minuta von Zieten, RAYMOND, 1946, pp. 239–30, pl. 2, 7–8.

The following dimensional formula is based on two populations from different German Upper Triassic horizons.

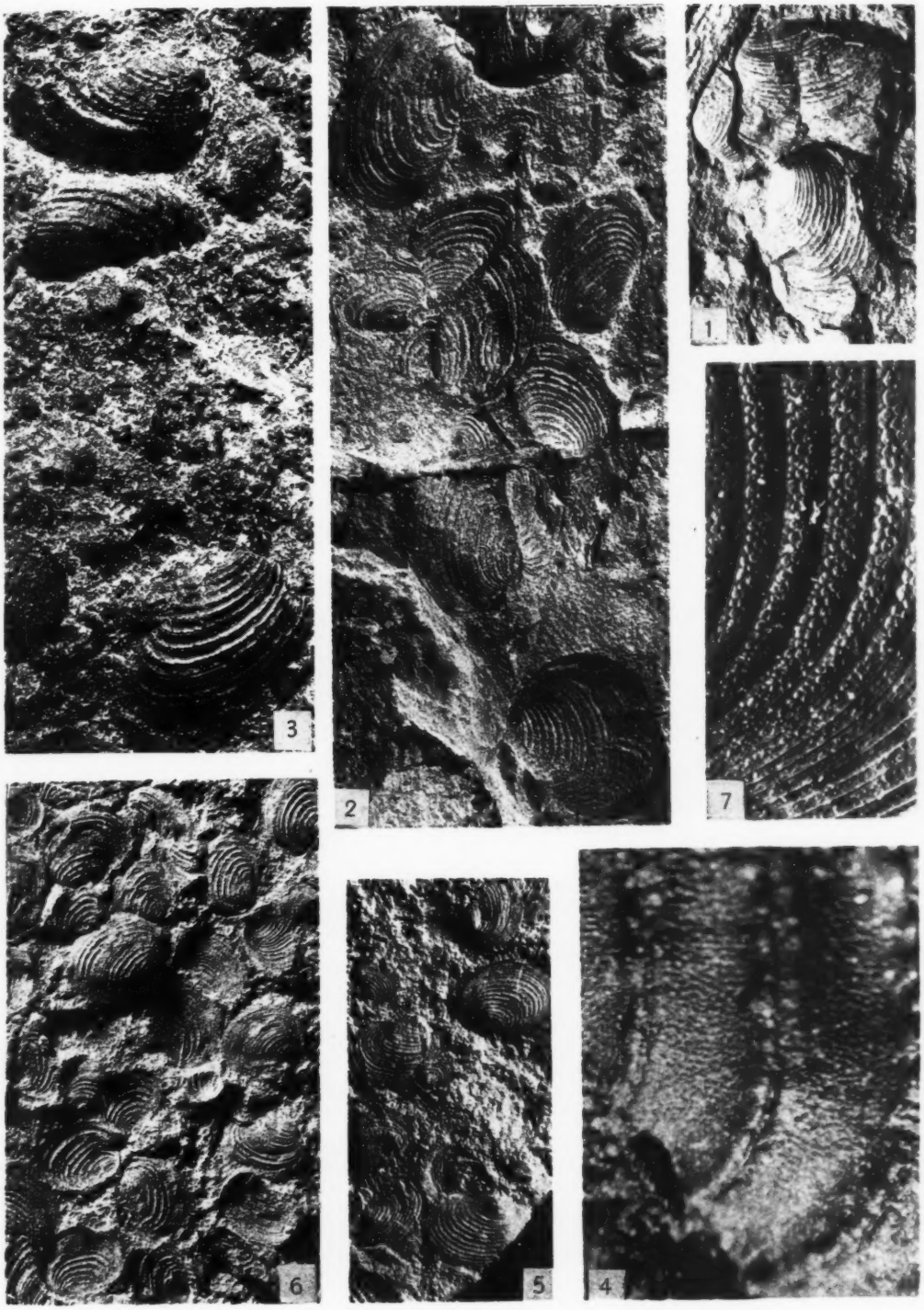
No.	Location	Dimensions		Ratio	Segments Total No.	Interspace mm. max.	Growth line mm. max.	Hinge line mm.	Sex	Valve Surface
		Lgth. mm.	Hgt.							
200106	Middle Keuper	3.5	2.4	1.5	9-8-3 20	0.2	0.04	2.1	female adult	right inside
200106	Middle Keuper	4.0	2.5	1.6	8-7-2 17	0.2	0.05	2.2	female adult	right inside
200106	Middle Keuper	1.5	1.0	1.5	8-1-8	0.1	0.02	0.7	juvenile	right inside
200107	Lettenkohle	3.2	2.0	1.6	7-7-14	0.25	0.06	0.2	female adult	right inside
200107	Lettenkohle	3.2	2.5	1.3	7-8-15	0.25	0.06	1.4	male adult	right inside

Discussion.—The dimensions of the two forms, of which the first one was found in the middle Keuper of Oehningen, Württemberg, and the other one in the Lettenkohle of Württemberg, Germany, vary slightly, however, in normal limits. The α-(male) and β-(female) forms are identified by their ratio, the latter being somewhat broader. The form which Picard (1911, pl. 23, fig. 2) described, is roundish and probably an α-(male) form. Jones (1862), pl. 1, figs. 28, 29 seems to have illustrated both types. The juvenile form of *Isaura ovata* (Lea) is hardly distinguishable from an adult *Isaura minuta* (Goldfuss). If mixed populations are available, mistakes can scarcely be made. The poorly preserved specimens, which the author (1946) believed to be "*Estheria*" *minuta* (Goldfuss) are now assigned to *Isaura ovata* (Lea). The former species must be considered to be still undiscovered in America, although *Isaura midlothianensis* comes close in size and sculpture.

The surface pattern of "*Estheria*" *minuta* (Goldfuss) (pl. 11, fig. 7), which could only be faintly detected on the specimens of the two populations figured, is that of Gross (1934, p. 311, fig. 7), showing a typical reticulate sculpture, which is almost identical with that of the living *Cyzicus californicus*

EXPLANATION OF PLATE 11

FIGS. *1–4*—*Isaura ovata*.—Lea's type specimen. Outside view of a right and left (female) valve from the Upper Triassic (Lockatong) of Phoenixville, Pennsylvania. Holotype of species. ×4. (p. 66)
2, Population of adult and juvenile valves (male and female) from the Upper Triassic (Lockatong) near North Wales, Pennsylvania. ×4. (p. 66)
3, Population of adult (female) valves in hard argillite from the Upper Triassic (Lockatong) near Edison, Pennsylvania. ×4. (p. 66)
4, The same as *3*, showing tubercular sculpture on the exterior surface. ×24. (p. 66)
5–7, *Isaura minuta* (Goldfuss). *5*, Mixed population of males, females and juvenile forms from the Lettenkohle of Württemberg, Germany. ×4. (p. 68)
6, Mixed population of the middle Keuper of Württemberg, Germany. ×4. (p. 68)
7, Typical reticulate pattern (viewed from the left side) and terminal growth lines. (After Gross). ×45. (p. 68)



Bock, American Triassic estherids

1

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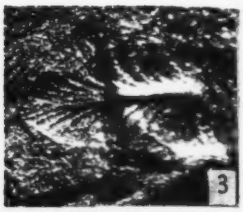
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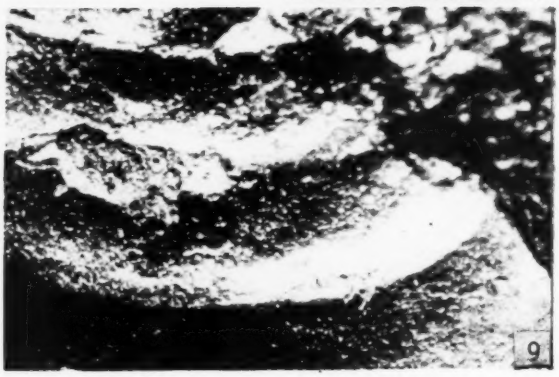
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Bock, American Triassic estherids

Packard (#12001, Crust. Coll. ANSP).

The taxonomic standing of *Isaura minuta* (Goldfuss) has also been the subject of extended discussions. Jones attributed the species to Alberti. He did not mention "*Estheria*" *germari* Beyrich (1857, p. 377). The latter author separated "*Estheria*" *minuta* of the German Keuper from the estherids of the Buntsandstein, which, he claimed, have a longer hinge line. Picard (1909, pp.618–19) upheld Beyrich's separation; but he recognized as the Buntsandstein species "*Estheria*" *alberti* of Voltz, who had pointed out the difference previously. "*Estheria*" *minuta* has been properly awarded to Goldfuss by numerous German investigators. Raymond (1946, pp. 239, 40) is of the opinion that von Zieten (1833) is entitled to the authorship, as he had published a figure, ascribing the species to Alberti. As von Zieten gave no description, the authorship remains better with Goldfuss. (International Rules Zool. Nomenclature, Art. 25).

ISAURA OLSONI Bock, n.sp.
Plate 12, figures 1–6

Description.—α-form (male). Shape oval, with straight hinge line, 0.7 mm. long, less than half of length. Number of segments 18. Valve length 1.5 mm., height 1.3 mm., ratio 1.2 mm. β-form (female). Shape elliptic to subrectangular; hinge line straight, half of valve length. All other margins well rounded, except umbonal margin, there forming a moderately rounded corner. 20 segments; length 2.2 mm., height 1.4 mm., ratio 1.5.

Identical traits.—Carapace voluminous; surface curvature pronouncedly convex, strongest in umbonal zone, slightly flattening out toward terminal zone: maximum diameter 0.8 mm.; test strong, about 0.01 mm. thick. Umbo dorsally-laterally arranged in anterior first quarter, slightly protruding over dorsal margin. Segments, varying little in number, consist of thin well-curved intervals, largest ones 0.14 mm. wide, and slightly raised growth lines, 0.015 mm. thick. The latter terminate tangentially in a trunk-like, roundish, hinge line, 0.07 mm. thick, extending along the interior margin of the shell (pl. 12, figs. 3, 4). There are three growth zones, which are difficult to distinguish. The highly convex umbonal zone, with about ten segments, is followed by a slightly offset intermediate zone of about six gradually enlarging segments, which inconspicuously continue in the terminal zone of about four flattening out, growth rings, only narrowing slightly near the peripheral margin. Radial cross section of test cycloidal. Interspaces invested by radial bars or radial undulations, the pattern of which is less apparent on the exterior surface than on the inside, although it is distinguishable over the whole shell surface close to the hinge line.

Discussion.—This estherid has some superficial resemblance in its shape to *Isaura minuta* (Goldfuss) and *Isaura mitsuishii* (Kobayashi and Huzita), but is distinct in its small size and surface patterns. This robust shell is found in company with many well-preserved ostracods, particularly *Cypridea valdensis* Sowerby (Jones 1863, pl. 5, figs. 26–28), known from the North German Wealden formation.

Location.—The shells were found near Merida, Venezuela (collected by geologists of the Imperial Oil Company of Toronto, Canada), in blackish, laminated shale, believed to be of Rhaetic age or slightly younger.

Depository.—Academy of Natural Sciences, Philadelphia. Holotype no. 200108; paratype no. 200109–11.

EXPLANATION OF PLATE 12

FIGS. *1–6*—*Isaura olsoni*, n. sp.—*1*, Adult left valve (female), showing radial pattern between growth lines. Upper Triassic of Venezuela. Holotype (female). ×24. (p. 69)
2, Adult right valve (male). Upper Triassic of Venezuela, ×24. (p. 69)
3–4, Outside and inside dorsal view, showing growth line trunk and hingeline. Same location as *2*. ×24. (p. 69)
5, Juvenile forms with radial sculpture. ×24. (p. 69)
6, *Isaura olsoni*, n. sp. Typical population with ostracods. ×16. (p. 69)
7, 8—*Howellites winterpockensis*, n. sp. Mixed population from the Upper Triassic of Virginia, near Winterpock. ×4. (p. 73)
9—*Isaura midlothianensis*, n. sp., showing the outside surface of three growth segments with reticulated pattern. Upper Triassic of Virginia, Midlothian coal mines. ×24. (p. 70)

ISAURA MIDLOTHIANENSIS Bock, n.sp.
Plate 12, figure 9; plate 13, figures 9–11

Description.—Peripheral shape of valve oval to subtriangular, strongly convex, with outstanding, subcentral umbo, laterally arranged; carapace voluminous, double cone-shaped having a maximum diameter of about 3.2 mm. Length 3 mm., height 2.5 mm., ratio 1.2. No distinct growth zones; terminal zone of about two to three segments, slightly offset from the remaining, steeply arranged, valve portion; growth segments amounting to eight, gradually enlarging without reductions in the terminal zone; maximum width of segment 0.4 mm.; growth line inconspicuous; outside surface of concave segments thickened along vertical section of interspace by radial notches along the margin of growth line; inside surface of segments, convex, smooth; surface pattern distinct on both sides of test, being basically reticulate; exterior pattern an indented mesh structure, irregularly sized, hexagonal to squarish, changing to radial lines along the growth line margin; interior pattern reflex picture of outside sculpture, consisting of raised irregular polygonal sections, with a narrow indented margin, about 0.012 mm wide. The dimensional formula follows:

Type No.	Dimensions		Ratio	Segments No.	Interspace mm. max.	Growth line mm. max.	Hinge line mm.	Sex	Valve Surface	Pattern
	Lgth. mm.	Hgt.								
Holotype No. 200112	3.0	2.5	1.2	8	0.4	0.05	—	— adult	left outside	mesh
Paratype No. 200113	3.5	3.0	1.2	8	0.3	0.02	—	— adult	left inside	bossed
Paratype	1.2	1.0	1.2	6	0.15	0.01	0.6	juvenile	left outside	—

Discussion.—This rather rare species was found in a 6 centimeter long coprolite, in which the shells were pyritized, and well preserved, although none of them is quite complete. While the assembly consists of three nearly entire specimens and a number of fragments, it can hardly be considered to be a natural population; but, as no other shells were found in the coprolite, this estherid must have been a dominant food type where the marauding fish devoured it. Naturally, the environment is somewhat problematical. The specimens available did not show a pronounced dimorphism to be distinguishable. The juvenile specimen disclosed that only two segments were added during the adult growth period, suggesting the advancement of single segments, compared with the group expansion of the growth segments in other species, such as *Isaura ovata* (Lea). This new type is close to some estherids described by Raymond (1946, p. 276, in his incertae sedis section) as *Rhabdostichus*, particularly to *Rhabdostichus pulex* (Clarke) from the marine strata of the Middle Devonian. However, the exterior cycloidal convexity of this species is anomalous and may suggest some other type of shell. There is also some similarity to *Isaura minuta* (Goldfuss) and to *"Posidonia" ovalis* Emmons (1856, p. 323, figs. 1, 2). Most of the estherids which Emmons described have been grouped by Jones with *"Estheria" ovata* (Lea). As Emmons' species are shown without sufficient specific differentiation and are no longer available, Jones' assignment appears to be justified.

Location.—Upper Triassic of Virginia, Midlothian coal mines, Midlothian, Virginia. Age: Stubensandstein-Knollenmergel series, equivalent to the Brunswick formation of Pennsylvania.

Depository.—Academy of Natural Sciences, Philadelphia. Holotype no. 200112; paratype no. 200113.

Genus HOWELLITES Bock, n.gen.

Description.—Valve oval to subround; surface curvature moderately convex; carapace compressed except in the umbonal

zone; test thin; umbo projecting laterally; growth segments numerous; interspace flat or slightly curved; radial cross section of test undulating, cycloidal, flattening out toward the peripheral zone; surface pattern of interspace radial, radial anastomozing, or reticulate; peripheral growth zone large, with many narrow concentric growth segments. Type species: *Howellites princetonensis* Bock, n.sp.

HOWELLITES PRINCETONENSIS Bock, n.sp.
Plate 13, figures 1–3

Description.—The differences between the dimorphic forms are slight. α-form (male). Outline oval, egg-shaped to subround. Hinge line short, less than half of test length. Umbo lateral, slightly protruding between first third and center of hinge line. Length of adult shell 7 mm., width 5.5 mm., ratio 1.27. β-form (female). Shape slender ovate; hinge line half of valve length; umbo located in first third of hinge line, laterally arranged; length of adult shell 7 mm., width 4.4 mm., ratio 1.53.

Identical traits.—Both types have three growth zones in common, of which two are always distinguishable. The umbonal zone having about seven narrow growth segments, the intermediate zone showing distinct, moderately undulating, gradually enlarging, slightly ridged growth segments, about six in number, with a width of 0.4 mm. maximum and a large terminal zone with about 28 narrow segments; protruding thin growth lines, about 0.1 mm. wide, closely arranged and normally not maturing to full size. Cross section of carapace, undulating to cycloidal, flattening out toward the terminal zone. Valve thin, fragile, about 0.1 mm. thick. Carapace diameter moderate, about 1.5 mm. The dimensions of the type and paratypes follow:

Discussion.—This new species is easily distinguished from *Isaura ovata* (Lea) by its egg-like shape, flat, compressed appearance, pronounced distinction between the terminal and older zones, and the quite numerous growth segments, which are much smaller in the terminal zone than in the remaining ones. No specimens have been found in which the narrow peripheral segments expanded to a normal width. The only estherid which seems to resemble this species is *"Estherites" endoi* Kobayashi and Kido (1947, pl. 19, figs. 8, 9). It is somewhat smaller, of similar outline, considerably compressed, and has a large terminal zone with narrow-set, numerous growth lines. This Asiatic species may well fit into the new genus, *Howellites*. That the test of this new species is thin and frail is shown by numerous much smaller ostracods, which easily indented the estherid valves under the prevailing sedimentary pressure. No juvenile shells were found. This new species is quite abundant at Princeton and at North Bergen, New Jersey, where it often covers large surfaces with thousands of shells, in a dark, laminated shale. The Bergen specimens are well preserved, carbonized or phosphatized, while the Princeton material is frequently disintegrated by ferric iron oxide, often indicating merely an otherwise distinct outline.

Location.—Princeton, New Jersey, beneath the Princeton University Library, and North Bergen, New Jersey (in the Granton Quarry at 73rd Street), both in the Lockatong formation, Upper Triassic, correlated with the Schilfsandstein-Bunte Mergel series of the European middle Keuper (Upper Triassic).

Depository.—Holotype no. 200114 and paratype no. 200115 Academy of Natural Sciences, Philadelphia. Bock Collection

Type No.	Location	Dimensions Lgth. mm.	Hgt.	Ratio	Growth lines Total Number	Interspace mm. max.	Growth line mm. max.	Hinge line mm.	Sex	Valve Shape	Pattern Surface
Holotype	Granton Quarry	7	5.5	1.27	7-6-28 41	0.3	0.1	3.2	male adult	oval left	none outside
Paratype	Granton Quarry	6.5	4.9	1.3	8-6-21 35	0.3	0.08	2.5	male adult	oval left	none outside
Paratype	Princeton	7	5.5	1.3	7-7-22 36	0.3	0.1	3.0	male adult	oval left	none outside
Paratype	Princeton	7	4.4	1.6	6-7-24 37	0.35	0.12	3.5	female adult	ovate left	none outside

Paratype no. 73862 in the paleontological collection of Princeton University.

HOWELLITES BERRYI Bock, n.sp.
Plate 13 figure 4

Description.—α-form (male). Valve oval to subround, broadest in anterior portion; margins well rounded, except hinge line, with slight extrusion of umbonal corner; length 5 mm., height 4.0 mm., ratio 1.25. Segments: 8-8-20. β-form (female). Valve subround, with straight hinge line, 2 mm. long, broadest in anterior section; length 3.7 mm., height 3 mm., ratio 1.23; segments: 6-8-22.

Identical traits.—Surface curvature moderate convex, compressed; umbonal zone slightly elevated; intermediate and terminal zone flattening out, but forming along the anterior margin a steep, convex shoulder; diameter of carapace reduced, about 1 mm.; test frail and thin, about 0.05 mm. thick; least resistant in umbonal zone. The umbonal and intermediate zones, which are difficult to separate, consist of slightly undulating, progressively enlarging, segments up to 0.15 mm. wide. The large terminal zone, covering about one half of the valve area with numerous, narrow flat segments. having a protruding growth line about 0.07 mm. wide, seems to represent the final growth stage.

Discussion.—This species is closely related to *Howellites princetonensis* n.sp. However, it is somewhat smaller and slightly rounder, which is indicated by the smaller ratio. Although the number of the specimens available, which were found in drill cores, was limited, the female seems to be more roundish, while in other cited species, this is a characteristic of the male. Therefore, it can not be precisely stated whether the dimorphism of this species represents sexual distinction or merely a form modification.

Location.—Upper Triassic of the Deep River Coal Basin, from core holes in the Cumnock formation, about 10 to 50 feet above the Cumnock coal, Chatham County, North Carolina. The blackish, dense sediments also contained remains of a species of *Bairdia* (*Candona*), scales of a semionotid fish and one of a coelacanth. The age corresponds with that of the Lockatong and is correlated with the Schilfsandstein-Bunte Mergel series of the European middle Keuper (Upper Triassic).

Depository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype no. 200116; paratype no. 200117.

HOWELLITES COLOMBIANUS Bock, n.sp.
Plate 13, figures 5–7, 12

Description.—α-form (male). Shape oval-elliptical with well-rounded margins; umbo lateral, inconspicuous within anterior third and middle. Hinge line 2 mm., less than half of length; segments 8-8-12, total 28; length of shell, 5.2 mm., height 3.2 mm., ratio 1.6. β-form (female). Shape elliptic subrectangular, margins well rounded; hinge line 3 mm., half of valve length; umbo moderate, lateral, one-third from anterior margin; segments 8-8-10, total 26; length 6 mm., height 2.8 mm., ratio 2.2.

Identical traits.—Surface curvature moderate, compressed, but evenly flexed over the whole shell; maximum diameter in second portion of umbonal zone, amounting to 1.1 mm.; test frail, thin, about 0.05 mm. with least resistance in umbonal zone; growth segments consist of a slightly protruding growth line, 0.04 mm. thick, and wide intervals, maximum width 0.3 mm., only slightly curved cycloidally or wrinkled; segments do not form undulations; umbonal zone moderately convex with about eight narrow growth segments; intermediate zone largest, with increasing width of the segments of the same number; terminal zone narrow, segments becoming abruptly closely set, forming a steep, convex, anterior-ventral margin. The terminal segments are covered with radial striae between the growth lines, about two radials per width of segment, changing to a vague pattern in the intermediate zone, having a coarsely radial, anastomozing, occasionally reticulate, appearance (pl. 13, fig. 7).

Discussion.—This new species fits well in the genus *Howellites;* yet it is distinguished from *Howellites princetonensis* n.sp. by the absence of sinuous undulations, the presence of strong radial sculpture, and considerably more elongate shape. There is also some slight similarity to the Japanese "*Estherites*" *kyöngsangensis* Kobayashi and Kido (1947, pl. 18).

Location.—Many specimens were found in gray-bluish, brittle shale near Montebel,

Colombia (Loc. G.1818. Imperial Oil Company of Toronto, Canada). Age: Rhaetic or slightly higher.

Depository.—Academy of Natural Sciences, Bock Collection, Philadelphia. Holotype no. 200118; paratype no. 200119.

HOWELLITES WINTERPOCKENSIS Bock, n.sp.
Plate 12, figures 7, 8

This type is one of the few estherids found as a population in reddish-brown hematitic shale, in which also ganoid fish scales with remains of the typical Virginia flora are abundant. It is quite diminutive, however, sufficiently distinct to group it safely with *Howellites*.

Description.—α-form (male). Test roundish, having well-curved hinge line, about 1.2 mm. long. Umbo central-anterior, inconspicuous. Valve length 2.4 mm., height 2.2 mm., ratio 1.1; 19 segments: 7-5-7. β-form (female). Shape oval; hinge line straight or slightly curved; all other margins well rounded. Umbonal zone nearly subcircular. Valve length 3.1 mm., height 2.3 mm., ratio 1.4. 21 segments: 7-6-8.

Identical traits.—Carapace compressed, having moderate thickness, about 0.5 mm. Test thin, fragile, forming around anterior margin ridge-like enlargements. Three growth zones distinguishable; umbonal with seven inconspicuous segments, about 0.1 mm. wide, comprising one quarter of total valve surface; the intermediate zone averages six, twice as large, segments, and the terminal zone eight, which gradually diminish in width. Radial cross section semicycloidal to undulating, well curved as a whole in the umbonal zone, flattening out toward the terminal zone. The following table gives the data for three specimens:

Discussion.—This tiny estherid is readily recognized as a *Howellites* due to its compressed, thin carapace, shape, and zonal arrangement. In size it is only slightly smaller than *Isaura minuta* (Lea); but the latter has less growth lines and it is rarely found to be subcircular, and as its carapace is more voluminous, having a well curved, full, anterior section, it does not require the ridge-like anterior marginal reenforcement of the *Howellites*, the purpose of which was probably to provide sufficient space for the more bulging head and frontal processes. In shape and structure, although considerably smaller, this new species resembles superficially "*Estheria*" *minuta*, as illustrated by Depéret and Mazeran (1912, pl. 5, figs. 2, 3 and 5). However, the type shown by the French authors is very unlike the true *Isaura minuta*. Depéret and Mazeran's species is considerably larger and flatter, has more growth segments, and shows a faint radial pattern on the peripheral segments. The authors' vague description also fails to shed any light on the differences apparent in their illustrations.

Location.—Upper Triassic of Virginia, near Winterpock. Age: Stubensandstein-Knollenmergel series.

Depository.—Academy of Natural Sciences, Philadelphia, Bock Collection. Holotype no. 200120; paratype no. 200121.

Genus ESTHERIELLITES Bock n.gen.

Description.—Carapace elliptical to subround, compressed, slightly elevated at the umbo, which projects laterally. Growth sections numerous, widest at intermediate zone, crowded at terminal zone; growth lines thin, interspace flatly arched; exterior surface of test covered with closely set,

Type No.	Location	Dimensions		Ratio	Growth lines - Total Number	Interspace mm. max.	Growth line mm.	Hinge line mm.	Sex	Valve Shape
		Lgth. mm.	Hgt.							
Holotype	Winterpock	2.4	2.2	1.1	7-5-7 19	0.2	0.05	1.2	male adult	round left
Paratype	Winterpock	3.1	2.3	1.4	7-6-8 21	0.18	—	2.2	female adult	oval right
Paratype	Winterpock	1.3	1.2	1.1	7-0-0	0.1	—	—	male juvenile	round right

solid, radial growth striae, fully covering ventral portion, becoming less conspicuous toward dorsal section. Genotype: *Estheriellites elliptoideus* Bock (emend.).

ESTHERIELLITES ELLIPTOIDEUS
Bock (emend.)
Plate 13, figure 8

Estheriella circularis BOCK, 1946.
Estheriella elliptoidea BOCK, 1946.

Description.—α-form (male). Valve oval to subround, broadest in anterior portions; margins well rounded, slightly acute at umbonal corner. Length, 5 mm., height 4.5 mm., ratio of 1.1. Segment formula, 6(?)-6-7, total 21. β-form (female). Valve oval to elliptical; hinge line straight, larger than height of test. All margins well rounded. Length 6.1 mm., height 3.2 mm., ratio 1.9. Segment formula 6(?)-6-14, total 26.

Identical traits.—Surface curvature moderately convex, flattening out toward ventral portion. Maximum diameter of carapace small, about 1.5 mm.; test frail, thinnest in umbonal portion, which is rarely preserved; umbonal and intermediate zones flatly cycloidal, with largest segments 0.5 mm. wide and corresponding growth lines 0.05 mm. thick. Terminal zone segments crowded, narrow, flat, covered with radial striae of roundish, minute, bars about 0.5 mm. thick, closely set, 12–20 per mm., which extend mostly uninterrupted over the whole terminal zone, being gradually disconnected in the following zones, there chiefly investing the top of the growth lines only.

Discussion.—In the light of recent disclosures (Kobayashi and Huzita 1943 and others) the two species, *Estheriella circularis* Bock and *Estheriella elliptoidea* Bock, were re-examined and were combined in the new genus *Estheriellites*. The form divergency of these two species follows closely those of other estherids, which were considered bisexual varieties. The new genus was chiefly established to distinguish the morphological and independent nature of the radial striae from those radials which are mainly structural, as they are in *Leaia* and *Estheriella*, to be discussed later. These should also not be confused with radial elements, which are distinctly separated by the growth line representing a radial pattern within the interspace, as in *Isaura olsoni*, n.sp. and *Howellites colombianus*, n.sp. However, there is a close resemblance of our species to the latter in other general features. The radial growth striae are thought to represent a protective cover of the newly developing segments, and are later on shed or disconnected during the process of expansion, reminding one of a secondary molting process, which is otherwise apparently unknown in the development process of the Conchostraca (Raymond 1946, p. 224).

This new genus appears to be similar to the genus *Dadaydedeesia* Raymond (1946, p. 260), in whose generic definition mention of "radiating lira" appears. The same author established *Estheriella radiata* (Salinas) *var. multilineata* Jones (1905) as the genotype, stating that it had "parallel linear furrows radiating from the umbo." Similar furrows are shown in *Estheriella costata* Weiss (Picard 1911, pl. 23, fig. 7), which Raymond also included in the genus *Dadaydedeesia*. These radial grooves seem to depress the concentric ribs at the point of intersection, causing a minute tile-like pattern. Obviously, a "furrow" can not be identical with a "lira" and it is suggested that Raymond's generic description should be confined to the differentiating element disclosed by his type specimen.

Depository.—Academy of Natural Sciences, Philadelphia, Bock Collection. Holotype nos. 16847, 8; paratype no. 200122.

Family LEAIAIDAE Raymond, 1946
Genus ESTHERIELLA Weiss, 1875

WEISS, 1875, p. 711.
JONES, 1891, pp. 53–57, pl. 2.
RAYMOND, 1946, pp. 257–260.

To determine accurately in which family the genus *Estheriella* Weiss belongs, the diagnosis of Weiss (1875) should be scrutinized. The main characteristic which distinguishes this genus from the common estherids is the presence of radial ridges, or riblets, of varying number on the exterior convex face of the test, which form furrows on the inside of the shell. The latter observation of the interior surface is morphologically important, although few investigators have taken notice of it. Picard (1919, pp. 618–22), who re-examined some of the original specimens of the German estherids,

did not mention this distinction, but he figures the genotype, *Estheriella nodosocostata* Giebel, with five radial main ribs, *Estheriella lineata* Weiss and *Estheriella weissi* Picard, with respectively seven and twelve ribs. Thus, the number of the radials chiefly distinguishes these species, while the hollow structure of these elements separates this genus from *Dadaydedeesia* Raymond, which has radial grooves, and *Estheriellites* n.g., which has solid radial growth striae. Leriche (1932) described *Estheriella moutai*, which is doubtless a true *Estheriella*.

Jones (1862, pp. 116–17), deserving again the credit of having recognized the crustacean nature of another new bivalved group, established it as the genus *Leaia*, characterized by "two conspicuous ridges hollow within." Raymond (1946, p. 280), forming the family Leaiaidae, based the latter on "two or more radial carinae, the areas between being concave." He did not indicate that the carinae were hollow, nor did he show that the areas between the ridges were concave, although he pointed out (p. 294) that this feature distinguishes the *Leaia* from the true *Estheriella* and that the ridges of the latter are in the median portion, whereas in the Leaiaidae all are equally prominent.

In his new genus and species, *Hemicycloleaia aselyi* Raymond (p. 288), states that the whole test surface is convex, an observation which can be largely verified for most of the species shown on his plate 6. Evidently this genus does not belong in the Leaiaidae, or else his restrictions for the family, that the areas between the ridges are concave, is not conclusive.

Technically, two close ridges must form a concavity. However in the case of this estherid bivalve, whose exterior surface is convex in order to be biologically functional, the broad convex surface between two widely spaced ridges may flatten out; but if the whole intermediate area were concave, this shell could not properly close its valves with its present structure.

The genus *Estheriella*, with its more numerous ridges, should be the least likely to show the natural surface convexity, due to the close arrangement of the radials. As Picard's figure of the genotype (1909, pl. 23, fig. 4) indicates a disposal of the five radial ridges over the whole test surface, no main distinction between this genus and *Leaia* that is pointed out by Raymond (1946, p. 294) remains with the exception of the number of the ridges.

The genus *Praeleaia* Lutkevich (1929, p. 724, pl. 26), having four to five carinae, and included by Raymond (1946) in the Leaiidae, is closely related to *Leaia* and *Estheriella*, overlapping in the number of the ridges the latter genus. The hollow nature of the ridges of *Leaia*, observed by Jones, is also clearly visible in the type population shown by Raymond (1946, pl. 16), the furrowed form of the members of which, shown on the interior surface of the shell, is identical with that indicated by Weiss (1875) for the genotype of *Estheriella*. As the hollow carinae remain the outstanding characteristic of *Leaia*, *Praeleaia*, and *Estheriella*, which are fundamentally only distinguished by the number of these structural elements, no good purpose would be served by assigning these genera, based on a definite, arbitrarily selected, number of radials, to different families. *Estheriella* is a natural genus of the Leaiadidae, however artificial the family may be in its own way.

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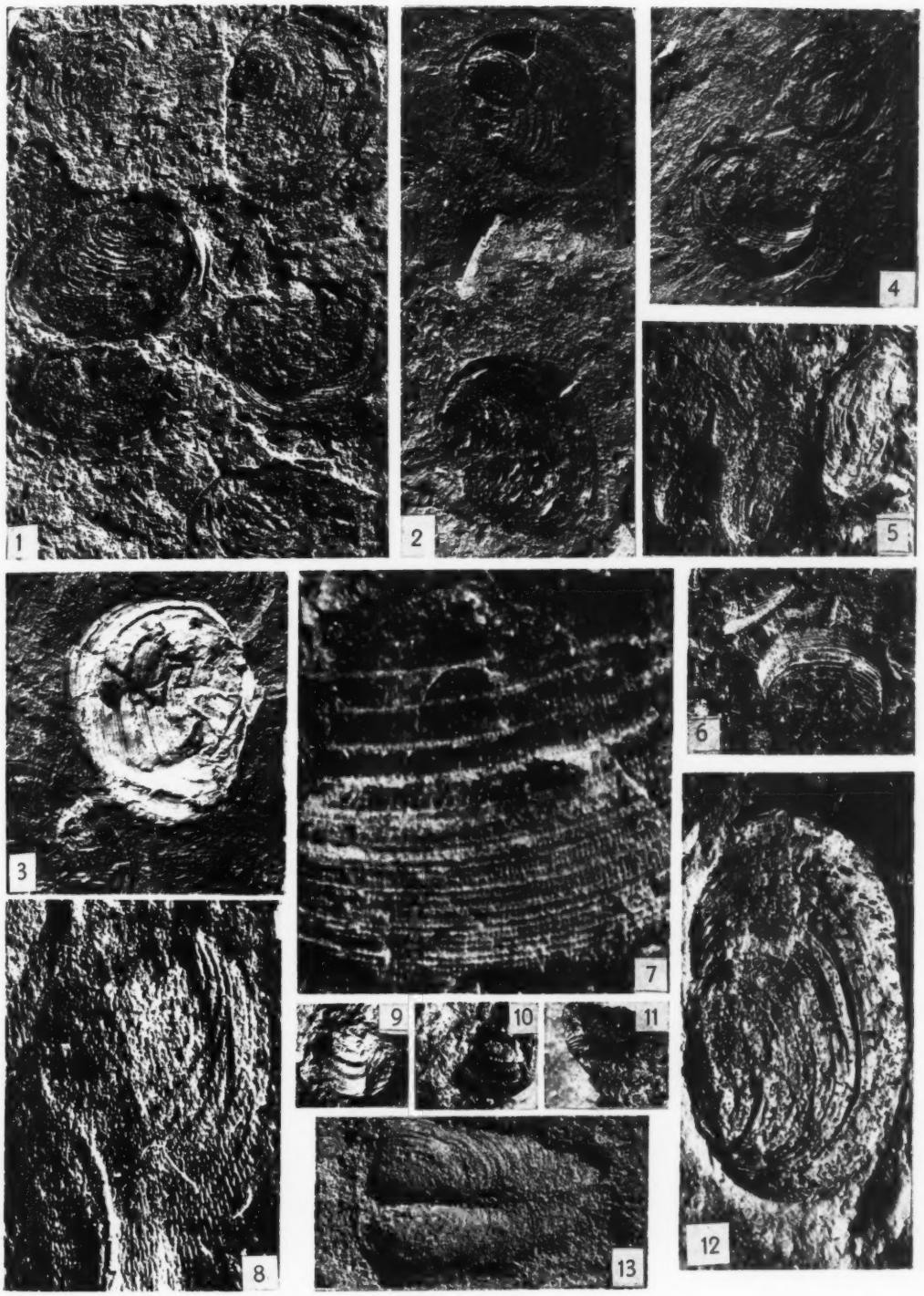
EXPLANATION OF PLATE 13

FIGS. *1–3—Howellites princetonensis*, n. sp.—Typical population of adult specimens. Upper Triassic (Lockatong). Princeton, New Jersey. ×4. (p. 71)
2, Two left female valves, showing distinct growth zones. Upper Triassic of North Bergen (Lockatong), New Jersey. ×4. Holotype. (p. 71)
3, Large phosphatized valve. ×4. (p. 71)
4—Howellites berryi, n. sp. Left and right valves of different type. Upper Triassic, North Carolina, Deep River Basin. ×4. (p. 72)
5–7—Howellites colombianus, n. sp. *5*, Two adult females and one juvenile shell from the uppermost Triassic of Colombia. ×4. (p. 72)
6, Male valve. ×4. (p. 72)
7, Enlargement of fig. *6*. ×35. (p. 72)
8—Estheriellites elliptoideus (emend.) showing radial growth striae. Upper Triassic (Lockatong) near Tradesville, Pennsylvania. ×16. (p. 74)
9–11—Isaura midlothianensis, n. sp. *9*, *10*, Portions of inside and outside shell, Upper Triassic of Virginia, Midlothian coal mines. ×16. *11*, Juvenile specimen. ×16. (p. 70)
12—Howellites colombianus, n. sp. Large female shell from the uppermost Triassic of Colombia. ×10. (p. 72)



Bock, American Triassic estherids

La Rivers, Nevada Pliocene frog

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, PP. 77–81, PL. 14, 1 TEXT FIG., JANUARY 1953

A LOWER PLIOCENE FROG FROM WESTERN NEVADA

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ABSTRACT—The anuran *Rana johnsoni* sp. nov. is described from a nearly complete specimen preserved in diatomaceous strata interbedded with the lower section of the Kate Peak andesite in west-central Nevada. An associated flora indicates a lower Pliocene age.

SYSTEMATIC DESCRIPTION

RANA JOHNSONI La Rivers, n. sp.

GENERAL *characteristics.*—A medium-sized species with the general facies of the modern *Rana pipiens* Schreber 1782,[1] but with a noticeably more massive head. No body outlines or skin impressions are detectable, and the fossil is incomplete, the hind extremities and one of the fore extremities being absent. The aspect is dorsal, the containing diatomaceous matrix splitting along the horizontal (frontal) plane. However, the dorsal features of the head are not available, since the plane of section lies between the maxillae and mandible so that the upper fragment shows the parasphenoidal surface of the cranium; the lower fragment, with the remaining discernible head structures, including tooth imprints, is the only one of the two head sections (upper and lower) which fits together with the body and leg blocks to reproduce the major characteristics of the animal. The mid-portion of the upper block is missing, but the availability of the two views (top and bottom) of the head and posterior portions helps greatly in obtaining adequate measurements. The animal has been distorted by dorso-ventral flattening (particularly noticeable anteriorly), and by shearing along the sagittal plane which has displaced the right side posteriorly with reference to the left side.

[1] This species is extant over all of North America, except the Pacific Coast, from northern Canada to central Mexico.

Skull.—While many portions of the skeleton are still represented by the bones in situ, the head itself is largely an impression only in the fine matrix; the sagittal shearing mentioned above is particularly prominent for this region. The maxillae and premaxillae are conspicuous by virtue of the regular and numerous tooth imprints in the matrix just exterior to the strong imprints of the mandibles. Both premaxillaries were slightly separated from the maxillae at the time of sagittal distortion. The pterygoids are prominent on both sides, internally adjacent to the thickened angulares of the mandible; the squamosals are weakly indicated on both sides. Both palatines are discernible, the right one occupying its approximate normal position, the left one displaced caudad by the sagittal shearage. External nares are detectable on both sides. Elements of the proötics are visible at the external bases of the cranium, and there are strong indications of a dorsal longitudinal median groove on the cranium. Exoccipitals cannot be detected with certainty.

Pectoral assembly.—Suprascapulae are indicated, but no scapulae can be seen. None of the ventral elements of the girdle are visible (clavicle, coracoid or sternum). Humeri are both present, that on the left side consisting of bone fragments and faithfully enough outlined to show the deltoid ridge and the distal articular surface with a faint condyle; the proximal head is buried beneath crushed skeletal fragments and its character is undiscernible. Only the left radio-ulna is preserved, its proximal articu-

EXPLANATION OF PLATE 14

Rana johnsoni La Rivers, n. sp. The holotype, ×0.7. From the lower Pliocene 6 miles north-northeast of Virginia City, Nevada.

lar surface pulled slightly away from the humerus, and the olecranon is visible; it appears (the radio-ulna) to be of typical shape, widening distally and showing the radio-ulnar groove. The hand has apparently been bent beneath the radio-ulna so that nothing distinctive can be noted about the carpals, metacarpals or phalanges, although fragments of the two latter are visible.

Vertebrae.—It is possible to count but seven of the nine vertebrae, all bearing conspicuous transverse processes or diapophyses. The two invisible vertebral elements are hidden beneath indistinct remnants of the suprascapulae. The sacral diapophyses are typically directed partially caudad, and, while distinctly more robust than those of the remaining vertebrae, are more-or-less parallel-sided with none of the noticeable distal dilation such as occurs in *Bufo* and more particularly in the Miocene Nevada toad, Taylor's *Miopelodytes gilmorei*. The urostyle is characteristically long and narrow, and twisted over on its side so that the lateral view is obtained; from this vantage, the dorsal keel, ventral thicker portion, and faint longitudinal groove separating the two, are plainly visible, as is the right zygapophysis, which is upturned as a noticeable tubercle. The diapophyses of the first two visible vertebrae (Vertebrae III and IV) are about the same length as those of the remaining vertebrae, but more robust; all diapophyses visible are approximately subequal in length. The sagittal shearage has depressed the diapophyses on the right side caudad with reference to those on the left.

Pelvic assembly.—The pelvic girdle has almost none of its original symmetry due to sagittal shearing and dorso-ventral compression, which has, as mentioned above, pressed the urostyle sideways and similarly displaced the left ilium. The ilia are unequally spaced from the urostyle, the left ilium being closest to it. The right ilium still retains its original dorso-ventral orientation to the rest of the body, articulates seemingly directly with the fragmented pubo-ischium, and has the same kind and degree of curvature as *Rana pipiens*. Sagittal shearing seems to have parted at least the dorsal wings of the pubo-ischium, and flattened them sideways; what little of their structure that remains apparent seems to indicate that the pubo-ischial system is typically *Rana* in size and shape and proportions. The cephalic ends of both ilia have been separated from the sacral diapophyses, the displacement being to the right. Both femora are present, but only the left one is complete; it is long, slim and delicate and a nearly exact duplicate of the gentle, sigmoid curvature of the *Rana pipiens* femur; acetabular and tibiofibular articulations are expanded in the usual fashion. The slim and delicately curved left tibio-fibula is the most complete one represented in the fossil, only its tarsal articulation missing. The only part of the right tibio-fibula which remains is a short segment near the distal end

TABLE 1.—COMPARATIVE MEASUREMENTS, IN TENTHS OF A MILLIMETER, OF FOUR ANURANS, THREE *Ranae* (RANIDAE, FROGS) AND A *Bufo* (BUFONIDAE, TOAD). THIS COMPARISON BETWEEN THE EXTINCT *Rana johnsoni* AND THREE EXTANT SALIENTIA DEMONSTRATES THE MANNER IN WHICH THE FOSSIL FROG FALLS WITHIN THE LIMITS OF VARIABILITY OF A PORTION OF THE LIVING GENUS *Rana*, AND SOME MEASURE OF HOW THEY DIFFER FROM A TYPICAL TOAD OF THE REGION.

	Lengths												Widths				
	Body	Skull	Humerus	Diapophyses III	IV	V	VI	VII	VIII	IX	Ilium[1]	Femur	Skull	Brain Case	Humerus[2]	Femur I[3]	Femur II[4]
Ranae:																	
Johnsoni	640	290	266	80	78	75	?	67	68	73	345	375	345[5]	60	41	14	38
Pipiens	625	230	203	60	45	41	39	36	36	40	315	376	280	55	37	14	39
Catesbeiana	1190	450	394	150	125	120	120	110	100	120	550	681	550	71	86	33	56
Bufo:																	
Boreas	620	220	250	65	70	62	42	38	31	59	280	290	270	70	55	16	50

[1] Measured laterally along the curve.
[2] Including deltoid ridge.
[3] Least width, dorsal surface.
[4] At distal head.
[5] Actual width *in situ*=450. 345 attempts to compensate for widening of head by crushing.

which has been pushed over on its side, showing the fused bones expanding toward the tarsal articulation, with the obsolescent grooving evident between the fused tibia and fibula. Unfortunately, nothing remains of the tarsal or foot bones.

Type locality.—In diatomite interbedded in the top of the Kate Peak andesite (Gianella, 1936), 6 miles north-northeast of Virginia City, Storey County, Nevada; approximately 119° 34′ W longitude and 39° 23′ N latitude (Univ. Calif. Mus. Pal. Locality V5204).

This locality, situated in rolling hills of

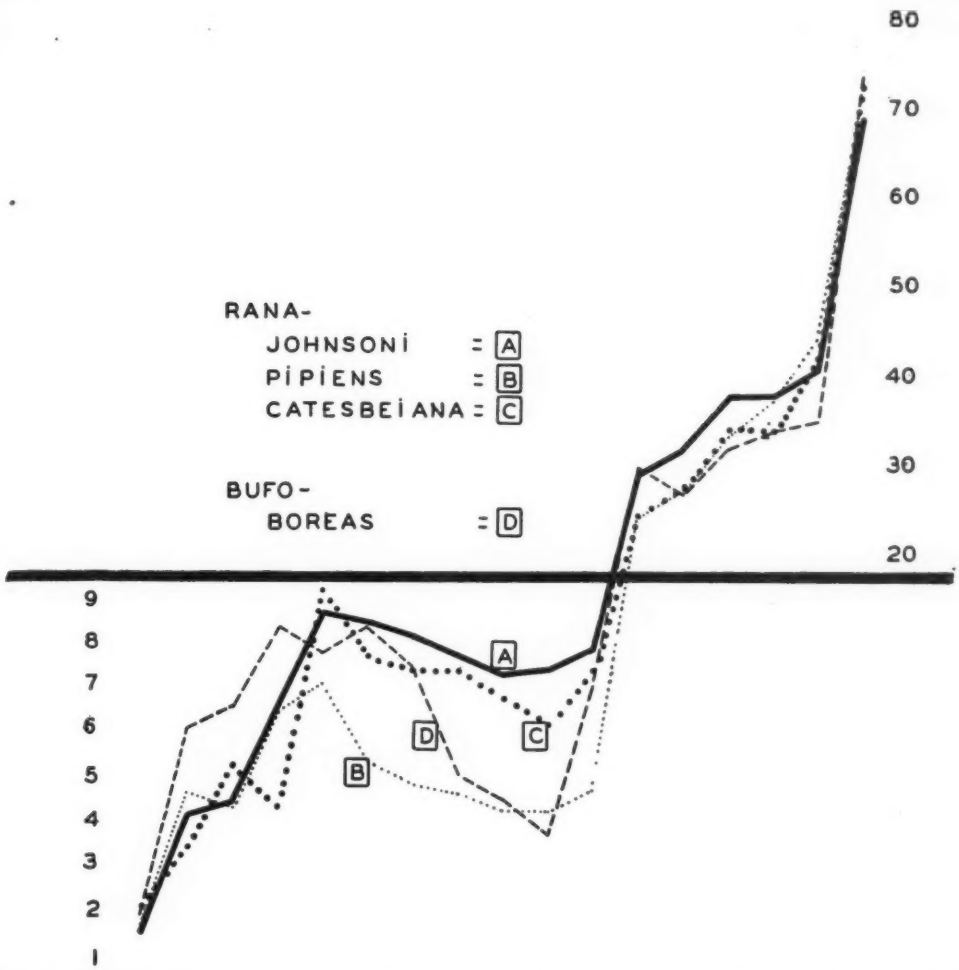

FIG. 1—Graphic presentation of ratio percentage comparisons between *Rana johnsoni*, *R. pipiens*, *R. catesbeiana* and *Bufo boreas*, computed on a baseline of combined body-skull length. Marginal figures represent the percentage scale, which breaks in the middle. Seventeen elements are plotted, as listed below in their left-to-right sequence:

1. Femur, least width.
2. Femur, width at distal head.
3. Humerus, width.
4. Brain case, width.
5. Diapophyses, lengths: III.
6. Diapophyses, lengths: IV.
7. Diapophyses, lengths: V.
8. Diapophyses, lengths: VI.
9. Diapophyses, lengths: VII.
10. Diapophyses, lengths: VIII.
11. Diapophyses, lengths: IX.
12. Humerus, length.
13. Skull, length.
14. Skull, width.
15. Ilium, length.
16. Femur, length.
17. Body, length.

the Virginia Range at an approximate elevation of 5800 feet, is reached via a mediocre road through a broken draw locally referred to as "Long Valley." It has yielded a good collection of plant materials, mainly leaves, which are presently being worked out by Dr. Axelrod, and he has informed me, in conversation and correspondence, that he considers the horizon as lower Pliocene in age. Chaney had previously suggested a lower Pliocene age for the "Truckee formation" of the Reno area (Gianella, 1936) on the basis of its flora. As Axelrod has indicated in correspondence, the conspicuous lacustrine diatomaceous exposures of the Reno area are not properly Truckee, as they have long been called, and will need a new formational designation.

Etymology.—The species is named for Mr. V. Kay Johnson, graduate biology student of the University of Nevada, who, with Mr. Dennis H. Hall, a former member of the Biology Department staff of the University, collected the specimen upon which the above description is based. Date of collection: May 23, 1951.

Disposition of type.—Deposited as No. 41276 in the collection of the Museum of Paleontology, University of California, Berkeley.

General considerations.—The "Truckee" diatomites of west-central Nevada are relatively rich in plant materials, but have yielded few animal remains. Exposures near Hazen (Churchill County), some 30 airline miles east-northeast of the *Rana johnsoni* locality, have produced large numbers of the funduline fish, *Fundulus nevadensis* (Eastman) 1917 (*Parafundulus*), and the stickleback *Gasterosteus doryssus* (Jordan) 1907 (*Merriamella*). While originally described as being in Lahontan (Pleistocene) lake sediments, these are actually, as Dr. Axelrod informs me, of so-called "Truckee" age. Stirton (1939) earlier suggested a probable Pliocene assignment for this locality on the basis of horse fragments.

The most recently lucrative discovery of vertebrate remains involving the "Truckee" lacustrines known to me has been that of the Brady pocket (Macdonald 1950), some 20 miles northwest of the type Truckee locality. Macdonald's short note mentions only the beaver *Eucastor lecontei* (Merriam) and the borophagine dog *Osteoborus diabloensis* Richey, as the two most important elements indicating a late Clarendonian (=late lower Pliocene) age. The main report dealing with the assemblage is still in press at this writing (March, 1952), and undoubtedly will include important additions to the meager list now available from previous investigations.

Few paleo-ecological deductions are possible on the basis of a single occurrence of *Rana johnsoni*. Dr. Axelrod writes that the flora of the type locality "is relatively humid, essentially middle Sierran, west slope," indicating, as we would expect, some change from present conditions. However, on that basis alone, there is no reason for supposing the environment of the type locality to have been otherwise than would be tolerated by present-day *Ranae*. While no member of the *Rana pipiens* complex occurs west of the Sierra Nevada mountains at the present time, such representatives of the genus as *Rana aurora draytoni* (Baird & Girard) 1852 and *Rana boylei sierrae* Camp 1917 occupy various habitats in the Sierras; the former extends up into the "Transition" coniferous zone and the latter is a high altitude type occurring in the southern Sierras above about the 7000 foot mark. Unfortunately, no skeleton of *Rana aurora draytoni* was available for comparison with *Rana johnsoni*. The former is characterized by a conspicuous broadness of head, and is somewhat more massive over-all than typical *Rana pipiens*. The possibility that *Rana johnsoni* was a member of the *Rana aurora* complex is somewhat stronger than that it was a segment of *Rana pipiens*, on evidence, meager as it is, furnished or suggested by anatomy, ecology and geography.

Rana johnsoni, to my knowledge, represents the first definitely Clarendonian vertebrate remains from the vicinity of Reno which have been complete enough to justify an unquestioned specific name. Fragments of horse and mastodont remains are occasionally recovered as float from "Truckee" beds between Reno and Verdi, but nothing more definitive has come to light among animals. No doubt these beds will produce a substantial microfauna when adequately investigated; I have noted an abundance of ostracod shells in "Truckee" diatomites just north of the *Rana johnsoni* occurrence.

Acknowledgement.—I would like to express my appreciation for the ideas gained in conversation and correspondence with Dr. Daniel I. Axelrod on various aspects of the so-called "Truckee" situation, as well as for his perusal of an early draft of the typescript on *Rana johnsoni*.

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, PP. 82–129, 7 TEXT FIGS., JANUARY 1953

THE EXTERNAL MORPHOLOGY OF THE TRILOBITE AND ITS SIGNIFICANCE

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ABSTRACT—The morphology of all the external organs is deduced in detail: it is found to reveal the stages of origin of the arthropod from a particular type of polychaet, and to indicate the relationships of the different classes of arthropods. A summary of 18 conclusions is given.

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1†. IMPORTANCE OF THE TRILOBITE

TRILOBITES have a unique morphological and phylogenetic importance, because they are so much the most primitive class within the arthropod phylum. They therefore indicate the mode of origin of this class: indeed, they suggest the nature of the prot-arthropod and its predecessor the pro-arthropod, and even something of the family relationships of the polychaet ancestor!

The prot-arthropod was not *Peripatus*. The Onychophora, after being included in the Arthropoda, were by Lankester (1910) made the lowest known grade of arthropod, which he designated Protarthropoda. This view of their position has been widely held. Borradaile (1935) and others made them the lowest sub-phylum of the Arthropoda, the Trilobita being the second; but perhaps the latest expression of opinion, L. Cuénot (in Grassé, 1949, pp. 1 and 36), places the class between the annelids and the arthropods; and states that it does not descend from the first, and is not the ancestor of the second. The position, there assigned, can be accepted; but though lack of relationship to the annelids is difficult to entertain, its application to the arthropods is fully supported below. *Peripatus* cannot be included in the arthropod phylum.

The trilobite, here claimed as the most primitive of known arthropods, and as having a head which had been formed by *one process* of coalescence of the anterior segments, is furnished with compound or radiate eyes; but that condition was preceded by a stage furnished only with simple eyes, here called the protarthropod. Because of their primitive character trilobites also suggest a new interpretation of the head of the various arthropod classes: and they reveal the origin

† References to parts of this paper are to the numbers of the sections.

of the tagmatism and nomomerism, so characteristic of some classes within the phylum

Trilobites hold an important place in the history of animal life, constituting the dominant fossils at the beginning of the record, i.e. in the Cambrian and Ordovician periods. It is possible, therefore, to read in some detail the morphology of their exoskeleton. They occur right through the marine Paleozoic, dying out in the Carboniferous and Permian; but even in the Lower Cambrian they comprise such diversity, that they must have had a very long previous history. Indeed here they already reach their greatest variety.

Though only their exoskeleton is available this is so closely related to the segmentation, musculature, and the distribution of various organs, that, by comparison with other primitive arthropods, much of the anatomy can be confidently inferred. As they left their exoskeleton to be fossilised, not only when they died, but also at all their numerous ecdyses, their larval ontogeny can also be traced in detail—from a minute protaspis (measuring in different genera between 0.25 mm. and 1.3 mm.) up to the adult of 6 mm. to 600 mm. (Raw, 1925, 1927; Störmer, 1941). In consequence, several phylogenetic series in the trilobites have been claimed; and even the mode of evolution of some arthropod organs is revealed. The writer was responsible a quarter-century ago for many revolutionary theories respecting them, and these are fully supported and greatly extended in the present paper, which however is no more than an outline, limited to the most primitive forms. The interested reader is recommended to read in advance, if available, the abstracts of the author's papers of 1924 and 1936A, as well as the short papers—1927 and 1937.

2. EXTERNAL SKELETON

Trilobites are peculiar in that the soft cuticle is not limited to the joints, necessary for motion between the segments, and between the segments of the limbs. Except for the exterior surface of the "hypostome" or labrum, and a border ("doublure"), primitively narrow, round the whole ventrum, the cuticle on the ventral body surface and appendages is soft, and only in very exceptional circumstances is it preserved at all. This contrast between dorsum and ventrum indicates that they habitually had the latter protected by the surface to which they were apposed, if not protected as in later forms by their own enrolment.

The distribution of armour, the character of their eyes mostly for vision all round the head, and their dominantly semi-ovoid body-form all suggest, that, for the most part, they had very limited locomotion; or at least attained only a very limited speed, as is the case in their direct descendant, the king crab.

Trilobites agree with Diplopoda and Chilopoda in possessing only one definite tagma, the head, and in exhibiting great variety in number of segments. In this they contrast with Malacostraca, Insecta and Arachnida, in which, besides the head, the body consists of other definite tagmata; and in which the segmentation is definitely limited; and also, except for some Arachnida seems to have been originally the same in each.

The trilobite body, it is true, is divisible into head, thorax of free segments, and pygidium of coalesced segments. But the pygidial segments, apart from fixation of their meso-terga and coalescence and fixation of their pleura into a relatively rigid shield, do not seem otherwise modified. On the other hand in the aberrant family Olenellidae no comparable pygidium exists. The normal pygidium perhaps originated as an aid to protection by enrolment; and it became perfectly adapted for this function. Analogous structures exist in the woodlouse (crustacean) and in the armadillo (mammal).

The relatively great strength of the hypostome even in the most primitive trilobites rather suggests that this part, which is homologised with the dorsum of the polychaet's prostomium (cf. Lamont 1949) was already protected by strengthened cuticle before its sub-retroversion i.e. in the pro-arthropod, when it would still form part of the dorsum. It is significant that the trilobite's hypostome is furnished with a narrow doublure as is the labrum of *Apus*, which resembles it much more than does any other modern arthropod. The sug-

gestion is, therefore, that the adult pro-arthropod was benthonic, with a dorsum, consisting of axial lobe and pleura, protected by strengthened cuticle. Further, the agreement of the biramous limbs of the trilobites' head with those of the post-cephalic body indicates that they had this character before the formation of the head, i.e. that the pro-arthropod was already furnished with biramous limbs on all its normal segments. On this view the phyllopodium of the lower Crustacea is attributable to neoteny.

3. PRIMITIVE CHARACTERISTICS OF TRILOBITES AND THEIR ORIGINS

Figures 1A–G

Their primitive nature is indicated by: I, the uniformity of the segments and appendages throughout the body; II, the retention of pleura throughout the body unreduced; III, the retention of a large hypostome; and IV, the retention of a soft ventrum. Regarding the first, even in the head in primitive trilobites the individual segments of the worm-like axis can still be seen and counted; and all but one (or two) of the known appendages of all the segments of the body are of the typical biramous character.

Characters of trilobites and of other arthropods indicate a derivation of the class from a polychaet bearing close relationship to the ancestor of the Polynoidae; and, as indicated by the paleontological record, this must have a colossal antiquity, and is discussed below. From the polychaet the arthropod inherited:—profuse segmentation and its segmental organs; its nervous system and sense organs, including segmental eyes from the peristome as well as from the succeeding segments, besides two pairs of eyes from the prostomium; a pair of antennae and anal cerci, besides the normal appendages, which in the interval between the polychaet and the pro-arthropod had acquired arthropodean character and were biramous; and pleura, which also are appendages, being derived from foliate lobes of the notopodium; and finally a periodicity in its segmentation. Also from the pro-arthropod it inherited axial spines on all the normal segments.

Comparative studies discussed below suggest that the mouth in primitive forms was above the *front part* of the hypostome leading up into the *foremost segment* of the glabella and that to right and left of the mouth an antenna was implanted. Behind it was an atrium, bounded above by the ventral membranous surface of the cephalon, interrupted by segmental pairs of appendages, and bounded below by the now dorsal membranous surface of the hypostome-labrum, which was free, but moulded upon the antennae, and so formed the sockets through which they curved to the exterior and to the front.

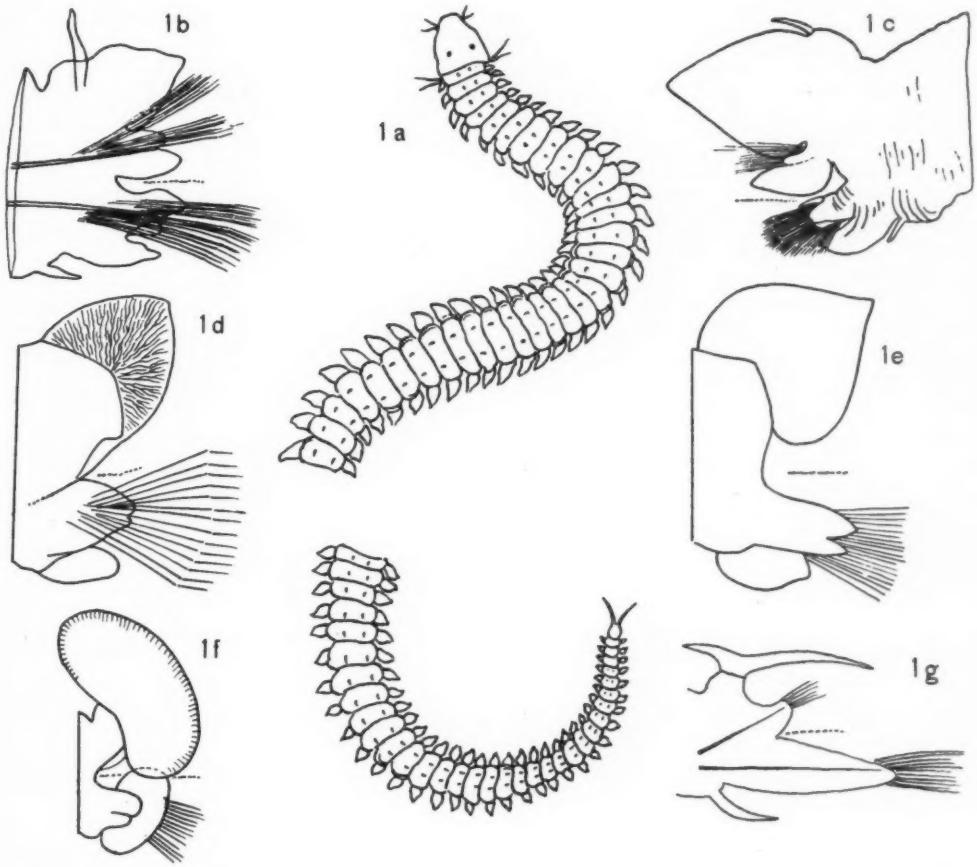
4. ORIGIN AND SIGNIFICANCE OF THE PLEURA

Most of these claims are substantiated below; but a note should be included here on the significance of the pleura already referred to. Zoologists following Bernard (1894, pp. 429–30) usually regard them as skin folds, which originated in the arthropod. But the writer claims: that these were inherited from the polychaet; that they are appendages, having been part of the worm's complicated parapodium; that in the early trilobites, as in the worm, they continued to be moved by muscles, as will be shown in a later paper; and that the movement in these same organs in the insect (for wings are pleura) has been developed until in the flight of the fly they effect 330 beats a second. Wings however are not regarded as having any community of origin with the legs; but though these two are now parted in the insect, the points of origin of the pleura in the segments of a trilobite are just above those of the legs.

That pleura are indeed primitive is indicated by several facts: their universal presence in the trilobite, which is much the most primitive arthropod class, and which had already reached its greatest variety in the Cambrian period; their presence in the other classes which are most primitive, namely the Merostomata, Crustacea and Diplopoda; their frequent presence throughout the body in early ontogenetic stages of the more primitive of the insects, and their presence even in the adult of the earliest insects known.

The pleura in primitive trilobites, such as the Olenellidae, Paradoxidae and Olenidae of the Cambrian, are each furnished

with an oblique backwardly directed "furrow," really a combination of ridge and furrow, which in the writer's view was closely connected with the distribution of its muscles, vascular system and nerves. This pleural furrow was inherited from the pro-arthropod, for in the early larval stages or protaspids in those families the pleural furrows still survive faintly on the inner part of the cheeks, and agree in spacing with the head segments indicated by the glabellar furrows (Walcott, 1910, pl. 25,



FIGS. *1A–G*, POLYCHAETA.

1A—Phyllodocid Polychaet, *Eteone picta* de Quatrefages: anterior and posterior parts of body of about 130 segments.

1B–G—Parapodia of Polychaets: *B* and *C* Nereidae; *D–F* Phyllodocidae; *G* Polynoidae. The dotted line opposite each separates the notopodium—above, from the neuropodium—below. All figures except *G* copied from McIntosh (1908), *G* from Hempelmann: (1934, p. 17) after Fauvel.

1B—Alitta virens Sars	.....	10th segment ×8
1C—Alitta virens Sars		37th segment ×8
1D—Eteone picta		30th segment ×140
1E—Eulalia sulosa Mont.		40th segment ×60
1F—Notophyllum foliosum Sars		×37
1G—Polynoe		

In *D*, *E* and *F* the foliate lobe of the notopodium is the only part of this left, and in *F*, is modified into a protective scale. In *G*, the elytriferous parapodium of a polynoid, the elytron is accompanied by a notopodial bundle of chaetae, with its aciculus (compare with *C*).

figs. 9, 10, 21 and 22; pl. 36, figs. 11, 12 and 14; pl. 38, fig. 24; pl. 43, fig. 6; Kiaer, 1916, pl. 6, fig. 1; Störmer, 1941, p. 83, fig. 9). The same occurred when segments coalesced into a pygidium. In both cases, what survived longest after the union was the pleural furrow, not the intersegmental boundary, because the first was connected with the musculature. This claim was early made by the writer (Raw, 1925, pp. 288–9; 1936A, pp. 68–9, or 1936B, pp. 292–3).

Störmer, however (1941, p. 105) accepting Bernard's theory that pleura originated with the arthropod as metameric repetitions of a sharp fold in the first segment, makes the following strange statement (p. 126): "Raw . . . following the current views on the segmentation of the trilobite body is forced to postulate that the interocular furrows are merely adaptations in close relation to the muscles. This leads to the impossible conclusion that the interocular furrows of the early larva in primitive trilobites have nothing to do with intersegmental division lines." It may be impossible to Störmer, who, "following the current view" does not derive the pleura from appendages moved by muscles. But he arrives also at numerous other strange conclusions, one of which falls to be discussed here. He accepts the writer's claim that the furrows on the interocular cheeks are homologous with the pleural furrows of the thoracic segments, but he also accepts the opposite view of Stubblefield—that they are intersegmental boundaries (in Raw, 1936A, pp. 68–9; or 1936B, pp. 292–3). He accordingly reaches the amazing conclusion that the present segmentation of the pleural lobes in this most primitive class of arthropods is entirely secondary throughout the body!

According to Störmer: 1, the head of the trilobite is not bounded behind by a segment; the occipital segment having half of its pleura in the thorax; 2, in the thorax the pleura do not belong to the segments to which they are attached; for in every pleuron only the inner-posterior half belongs to this, the anterior-outer half belongs to the segment in front; 3, the pygidium too anteriorly is not bounded by a segment!

It is because the pleural furrows on the interocular cheeks as well as throughout the body are curved, that Störmer reaches his amazing conclusion—that the pleura have been united, and later cut across by a new segmentation. But both the pleural furrows and the pleural boundaries are curved and increasingly so towards the rear (l.c., pp. 124–132; see below 15). Störmer claims too that he is supported in his view by the structure of *Limulus*. But *Limulus* offers no support; for, in marked contrast with the trilobite, it is specialised. Here the appendages of the first post-cephalic or "opisthosomatic" segment, the chilaria, have advanced under the head to close the mouth space behind, whereas the tergum of this segment has partly slipped under the head shield, or cephalothorax as it is called, without the pleura or any part of them joining the prosoma. But the regular segmentation of the trilobite at this junction of head and thorax, whether we view it from above, or from below (as seen in *Triarthrus* and *Neolenus*), shows us that nothing of the kind has happened here.

Störmer's claim involves the union of all the pleura into a pair of lateral folds and their later resegmentation on a new plan. But the most primitive segments of the most primitive trilobites—the posterior thoracic segments of Olenellidae, Paradoxidae and Zacanthoidae have their doublures coming practically to the dorsal furrows; i.e. these pleura are free: there is no reason whatever to believe that they were ever united, and there is no justification whatever for Störmer's claim. It may have seemed a waste of space to discuss it; but it is fundamental, for if Störmer were right, the author's comparison with the polychaet would be vitiated.

The most primitive pleura are to be sought in the rear segments of the thorax of early forms which are primitive in other ways, and especially in early stages of development of such forms. Except for the pleural furrow this shape of pleuron is closest approached among polychaets in the Phyllodocidae, which however in modern forms exhibit no periodicity in segments or appendages: *Eteone picta* de Quatrefages is a good example, mimicking both in the form and disposition of the notopodia the pleura of the primitive trilobite. (See figs. 1A–E.)

It is clear that Störmer derived his idea from Iwanoff (1933, pp. 309, 341) who de-

scribes the fate of the segments at the junction of the prosoma and opisthosoma of *Limulus moluccanus*. The writer was quite aware of this and had noted it in the Paleozoic eurypterids, where even in the fossils it is clear. But Störmer imports into the origin of the primitive trilobite what took place long afterwards in the origin of the specialised merostome. Iwanoff attributes the peculiarity to the mechanics of the body curvature. The writer attributes it to the forward movement of the appendages of the 7th normal segment to close the mouth space behind as will appear in his forthcoming "Origin of the Arachnida." Iwanoff would seem to have started with a theory of the relationship of the trilobite to the arachnoid and to have seen his embryology by the light of this theory. The early evolution of the pleura within the Trilobite is discussed below (15).

5. MODE OF ORIGIN OF THE ARTHROPOD REVEALED BY THE TRILOBITE

The mode of origin of the arthropod was by continued subretroversion of the prostomium and peristome (represented by the labrum or "hypostome" and the "rostrum" respectively) (Bernard, 1892). This led to fixation of the terga, and coalescence and fixation of the pleura, of the succeeding *six* segments. In this way was formed a cephalic tagma or head out of these *eight* elements: prostomium, which is highly compound (Raw, 1949, p. 14); peristome, which is not a true segment comparable with the rest (l.c., p. 26); and the succeeding six normal segments. This composition of head in the most primitive of known arthropods, which might therefore inherit up to nine or ten pairs of appendages and nine pairs of eyes, is not generally recognised by those zoologists who limit their attention to modern arthropods; but it is of great importance for their morphology, and is extensively discussed below.

The nature of this strange pose suggests that for the evolving arthropod there was then a period of peculiar safety. It constituted one of the greatest crises in evolution, and brought many changes in its train. It carried the brain immediately beneath the site that the ventral nerve cords, then lateral, were later to occupy; and it induced, as the writer believes, vast changes in the nervous system: it also initiated the transformation of the cephalic legs into mouth parts for all the arthropods except the arachnids s. l. or Chelicerates.

This head, comprising all the front of the body as far as the sixth normal segment is already present in the earliest larval stages of trilobites known, the protaspis, which must include also the anal "segment" or telson. It also corresponds in composition with a long stable stage in the pelagic larval development of the aproditid *Polynoe*, shortly before it settles on the sea floor (Häcker, 1895; De Saint Joseph, 1895): this is apparently also the case in *Lepidonotus* (Leschki, 1903). Hence the composition of the arthropod head was probably determined for it by the ancestral polychaet.

It has been claimed that the occipital segment, because of its frequent resemblance to the succeeding segments of the thorax, was therefore added after the rest (e.g. Richter, 1932, p. 842); but since this likeness is attributable to the muscular connection and movement between the two, there is no reason for such a conclusion especially in view of many new facts adduced below.

Independently of these considerations, study of the trilobites indicates, too, that the formation of the head was effected by one process, and that therefore all arthropods inherit the same head, constituted of the above named eight elements, the first of which, the prostomium, was highly compound in origin, whereas the second also was of unique character. Onychophora therefore should not be regarded as arthropods, and constitute a quite distinct phylum, as is suggested also by other characters.

The nature of the subretroversion of the anterior part of the body of the proarthropod which initiated the prot-arthropod can still perhaps be realised, though it must have taken place very long before the Lower Cambrian—the age of the earliest creatures in which we can see the effect. Though trilobites owing to their usual occurrence in shale are commonly pressed flat by settlement of the sediment, when they are preserved in sandstone or limestone they often retain much of their convexity. Especially is this the case in later forms with

strong exoskeleton. When so preserved, primitive Cambrian trilobites also, for example—olenellids and paradoxidids, are extremely convex, approximating in form to half a fowl's egg cut longitudinally, the cut surface being that applied to the sea floor. The head constitutes the quarter-sphere at the broad end, bounded behind and below by semicircles; except that, below, all round, the test is bent outwards to form a sledge-like base for resting on the sea floor. The axial lobe of the head or glabella thus curves down to the front through a quarter-circle, from horizontal behind to vertical in front; and this curvature is almost exactly continued in the somewhat sharper curve of the hypostome (also semi-ovoid in form); which hence projects down below the level of the marginal rim. If then this most primitive known class of the arthropods is an indication of the nature of the prot-arthropod, the subretroversion, which initiated this was by fairly uniform curvature. The sledge-like margin was a later development, determined by its mode of life (see fig. 6).

6. THE TRILOBITE CEPHALON

As the cephalon is the only definite tagma in the trilobite its composition is of prime importance. It has been, and is still, a subject of much controversy, though in the present outline it is not necessary to recount the successively expressed views, which has already been done by others. But no such claim of definite relationship between the polychaet and the arthropod, as is here advanced, has previously been made.

It is recognised that under the dorsal shield there is always a hypostome, and that primitively we have also a rostral plate between these, besides the seldom preserved articulated appendages. Those three parts—head-shield, rostrum and hypostome—are normally separated from one another by sutures of soft cuticle, and the rostrum also at its ends from the adjoining parts of the doublure as in *Calymene;* though any of these sutures may be lost by ankylosis, as are the connecting sutures in the Phacopidae, and the hypostomal in Olenellidae and some Paradoxidae. Further, the rostral plate may be stretched out to a half annulus as in the Olenellidae by the migration of the connecting sutures and neighbouring parts; or it may be reduced in length to any extent down to disappearance by approximation of the connecting sutures, until they meet, as in Olenidae, Asaphidae and Dicellocephalidae. The hypostome is generally recognized as homologous with the labrum of modern arthropods. The writer also claims it as the modified tergum of the prostomium, and the rostrum as the tergum of the peristome of the proarthropod and the polychaet. Curiously, there is still much difference of opinion as to how many segments the dorsum of the cephalon represents, and how these are to be homologised with those of other arthropods. Let us contrast the views in two of the latest papers on the morphology of the trilobite.

Richter (1932, p. 847 and fig. 5) recognises an eye segment and six other segments homologised with the first six appendage-bearing segments of the crustacean. The following is his scheme.

I. Eye segment; embracing ventrally the rostrum, and dorsally the pre-glabellar field and the free cheeks with the eyes.

II. Antennular segment (1st segment of glabellar "frontal lobe"); with the trilobite antennae, homologised with A1 of Crustacea.

III. Antennar segment; embracing 2nd segment of "frontal lobe" with eye ridge, and with the hypostome; its appendages (A_2) aborted.

IV–VII. The remaining segments of the rachis; homologised with those bearing mandibles, 1st and 2nd maxillae, and 1st maxilliped (on VII, the occipital segment). It is surprising to find Richter associate the hypostome with his segment III as if it were the sternum of a segment.

Störmer, who makes the Arthropoda polyphyletic, arising by eight different roots from the Annelida (1944, p. 143) makes the Trilobita the basal member of his "Trilobitomorpha," but leaving no descendants. He associates them with the Chelicerata, and is thus in the opposite camp from Richter. Störmer bases his views on the early development as interpreted by him. But he does not seem to realise that the early protaspids, because they have just escaped from the spherical egg are themselves subspherical, for he accepts all the protaspids as exhibited in the rocks as complete larval trilobites. Only those however of the Olenellidae are nearly complete,

exhibiting their complete eye-lobes and complete head margin. This is due to a horizontally extended body-form, probably attributable to their early settlement on the sea floor (Raw 1937, p. 595). All the other protaspids that he uses are manifestly incompletely exposed, not exhibiting the eyes nor the head margin except at the rear, where the cephalon must have been followed by the telson. His claim that they are complete is illustrated by his hypothetical drawings (1941, p. 85): the writer's claim, that they are not, was already made in 1925 (pp. 258–265) and 1927 (p. 240). Störmer does not acknowledge any reduction or loss of appendages owing to their cover by the hypostome (below, 12 and 13). He does not recognize the three pairs of head spines, claimed by the writer as primitive in trilobites, claiming that they do not appear till the meraspid stage. In this he is shown to be wrong by the ontogenetic series figured and described by Ross (1951) and discussed by Raw (1952). Also he ignores the probable control imposed by the spherical egg and the fact that his protaspids are incomplete. Regarding the number of segments he claims that, "the frontal lobe of the axis primarily comprises the axial portion of one segment" (l. c., p. 115); but "during larval development some part of the pre-glabellar field might probably become vaulted and united with the anterior glabellar segment, forming an expanded frontal lobe" (l. c., p. p. 119). It was Jaekel (1901) who first claimed that the trilobite's cephalic rachis embraced six segments; and he was followed by Warburg and the writer, quite unknown to one another, in 1925. Raw (1925, p. 232) also claimed, that the first dorsal segment bore the procranidial spines as its pleural spines, likewise the 3rd and 4th together bore the parial spine and the 6th bore the metacranidial spine (see below, 9).

Störmer's segmentation of the head is based not on the characters of the most primitive trilobites, but on the position of the "antennal pits," as he calls them, which are absent from primitive trilobites. "Anterior pits" is a much better name for them (Howell et al., 1947, p. 74): they are doubtless apodemes for the attachment of muscles, but there is no sufficient reason to believe that they indicate the antennal segment. Even if we knew that muscles from them moved the antennae, it would not indicate the antennal segment; for in these same trilobites there is very good reason to believe that the appendages belonging to the anterior segments of the glabella have been reduced and modified, and some of their muscles may have been appropriated by the antennae. The enormous variety exhibited by trilobites even if we limit our review to Cambrian forms shows how varied was the evolution that took place within the class: we may note for example the enormous variety of Cambrian forms described in the last decade by Rasetti (Rasetti 1944–1948), who is one among many.

Störmer's segmentation, abbreviated, is as follows (1941, p. 123 and fig. 17, p. 145):

Preoral. 0. The pre-antennal segment complex; comprising hypostome ?, doublure with rostrum, preglabellar field, lateral eyes, extra-ocular cheeks and genal spines† and secondarily probably the anterior part of frontal lobe of glabella, innervated from a "procephalon."

1. Antennal segment; comprising frontal lobe of glabella, eye ridges and palpebral lobes and a strip of cheek behind them; with antennae A1; innervated from a deutocerebrum.

Postoral. 2. First leg segment; comprising 2nd glabellar lobe with pleura on interocular cheeks; bearing 1st biramous appendages; innervated from tritocerebrum.

3. Second leg segment; comprising 3rd glabella lobe with pleura on interocular cheek.

4. Third leg segment; comprising 4th glabellar lobe with pleura extending into intergenal spines.

5. Fourth leg segment; occipital, with pleura forming the pleural spines of the first thoracic segment!

As regards the number of cephalic segments these two papers by Richter and Störmer differ in that, though both recognise an eye segment in front of the rachis, in the rachis itself Richter recognises six whereas Störmer recognises only five. Early writers basing their view on the study of later trilobites recognised no more than five, though many genera gave evidence of

† Notwithstanding that these may be any one of three different pairs (Raw 1925, 1927).

six. But when the Lower and Middle Cambrian faunas came to be described, it was found that among these were great numbers of genera exhibiting clearly six segments. In no less than sixteen families are found forms clearly exhibiting this number; and in several others the "frontal lobe" is so large as to suggest the same. That so many, and especially later forms fail to exhibit the anterior one (or more) furrows which indicate the segmentation, while retaining those behind, is attributable to the fact that except for the antennae the anterior appendages were extensively under cover of the hypostome which extended rearward so as to underlie all the rachis except the occipital segment in some, and all except that and the pre-occipital in others. The writer believes that, in *Triarthrus*, where both Beecher and Raymond claimed the presence of four pairs of biramous appendages under the cephalon, a further two anterior pairs must have been greatly reduced.

The distinction between these two papers is still greater when we compare their allocation of the segments and their appendages. Both writers homologise the trilobite antennae with the antennules A1 of the Crustacea; but whereas Störmer homologises the reputed four pairs of biramous appendages to the other four consecutive pairs of the crustacean head, Richter on the contrary believes that the appendages of the antennar segment A2 have aborted; and that the reputed four pairs of biramous appendages represent the mandibles to the 1st maxillipeds inclusive.

7. PRIMITIVE FEATURES OF TRILOBITES AND THEIR SIGNIFICANCE
Figures 2A–F, 3A–H

The development of the trilobites is of great importance for their interpretation. This however was discussed in considerable detail by the writer in 1924, 1925 and 1927. Nothing that has appeared since has given cause to modify the opinion then expressed; and hence it need not be repeated here. No creatures better illustrate the Biogenetic Law (Raw 1927, p. 143); but this must be used with discrimination. Four facts at least must not be forgotten: I, that all sexual reproduction involves development from a single cell; II, that the early protaspis has just escaped from a spherical egg; III, that, as suggested by a descendant, *Limulus*, the dorsum of the embryo probably extended over more than a hemisphere; and IV, that in all segmented animals the segments must multiply up to the number of the adult. Matthew, Beecher, Raymond and Störmer have all, the writer believes, gone far astray through lack of these considerations.

No trilobite as primitive has, as yet, better exhibited its meraspid ontogeny than the olenid, *Leptoplastus salteri* (Callaway); and it occurs in such abundance that one can be quite sure of the character of all the stages. At the time when the ontogeny was described, no protaspis had been discovered; and only one has been discovered since.

The conditions of occurrence are most favourable for study: the remains were flattened out in the shale, like those of the much later *Triarthrus eatoni* (Hall) (*T. becki* Green). There was, however, in the case of *L. salteri*, no comparable chemical change of the skeleton, and this has been dissolved away by underground waters. As also the remains occurred in such abundance on particular shale partings, the the rock parts just where they occur; and displays their form as external and internal moulds in great perfection. The protaspid stages of the ontogenies of other olenids, as

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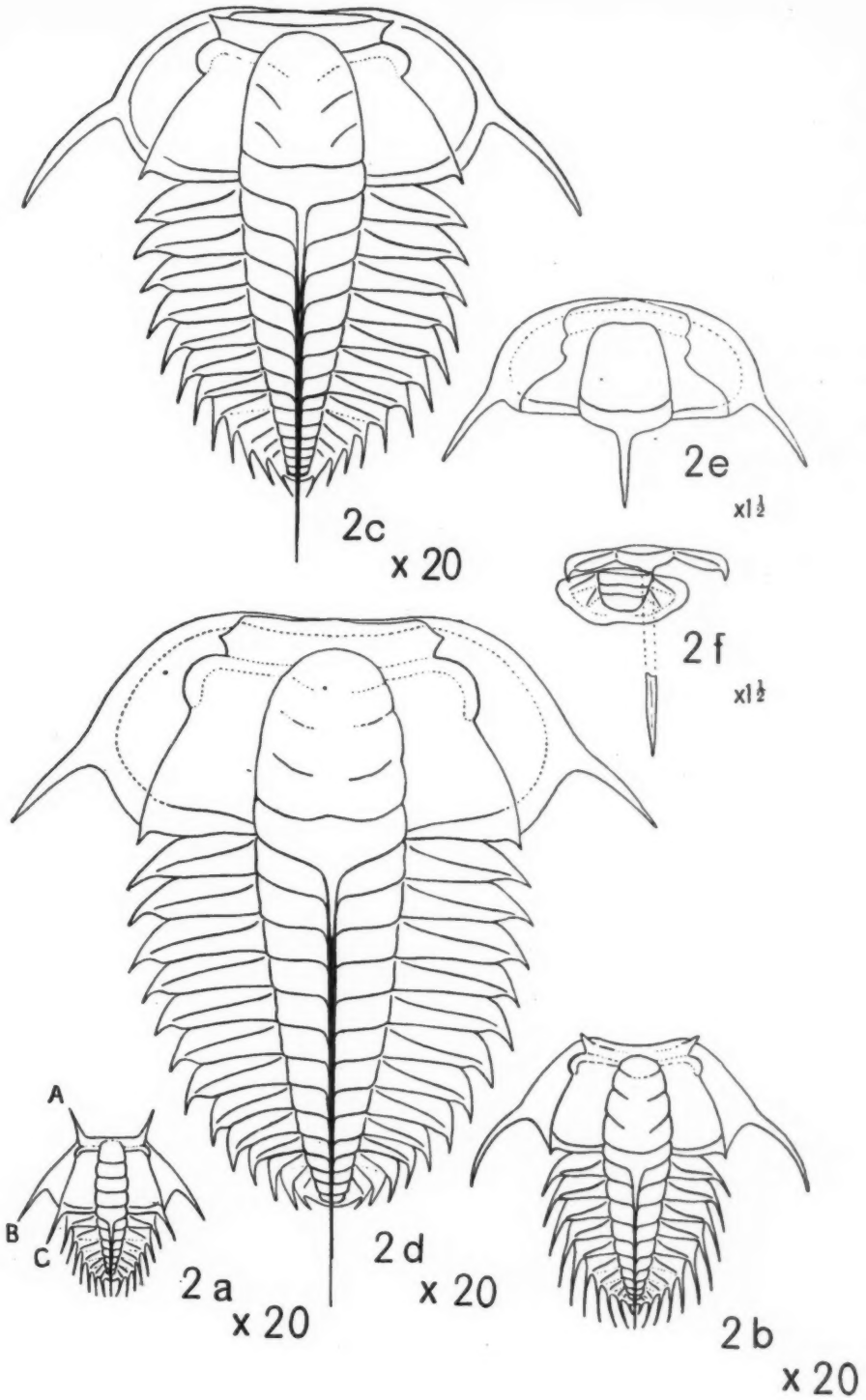
FIGS. *2A–F*—Meraspid and holaspid stages of development of the olenid trilobite *Leptoplastus salteri* (Callaway) original.

2A–D—Meraspid Stages ×20. *A*. Heptacicephalic Stage, Degree. 1. *B*. Ctenopleural Stage, Degree 5. *C*. "Transition" Stage, Degree 7. *D*. Autogeneric Stage, Degree 10.

2E, F. Late holaspid Stage or autospecific Stage ×4/3. *E*. Large cephalon. *F*. Pygidium and last thoracic segment: the latter bears a long axial spine, as do all the segments except those of the pygidium, which have also lost their pleural spines.

On the figure *2A A* is the procranidial spine, *B* the parial, and *C* the metacranidial. Note that all three pairs are traceable throughout except in *E*.

Reproduced from the author's 1927 paper (Am. Jour. Sci., ser. 5, vol. 14, p. 24). See also Raw 1925, pp. 248–257, pls. 15–18.


2c
x 20
2e
x1½
2f
x1½
A
B
C
2a
x 20
2d
x 20
2b
x 20

for example those described by Strand (1927) and by Poulsen are from limestone, and do not exhibit the peripheral spines: indeed, they could not do so, because they were more nearly spherical, like the embryos of *Limulus;* and because occurring in limestone they retain more of their original relief.

As ontogeny is so significant for morphology, that of *L. salteri* is represented here by five stages repeated from 1927 (see figs. 2A–F).

The first stage, 2A, has one segment in the thorax and six segments in its (transitory) pygidium. Its cephalon is on the whole one of the most primitive known. Its rachis, with long simple segments, recalls its annelidan ancestor; but it has lost all axial spines except on the occipital segment; and the anterior glabellar lobe, a coalescence of two segmental rings, has lost all trace of the anterior transverse furrow between the two segments, though it is still considerably longer than a single segment. This head is primitive in displaying all seven peripheral spines, the procranidial spines in front, the parial spines on the free cheeks and the metacranidial spines, together with the occipital spine, behind. It is however specialised in having a concentrated eye, and is adapted to its planktonic existence by having this far to the front and also by the development of the primitive peripheral spines for flotation.

The post-cephalic body is primitive in the narrowness of the pleural lobes, not much wider than the rachis, and in the presence, form, and length of the pleural and axial spines. The coalescence of six segments in a pygidium is a specialisation in comparison with its annelid ancestor.

In later development one may note:—the progressive reduction of the procranidial and metacranidial spines; that the segments all become relatively shorter in proportion, and especially those constituting the "anterior glabellar lobe," which narrows and changes in form to emarginate in front; and that the glabellar furrows become pairs of oblique furrows, which later disappear. This change is probably connected with reduction and specialisation of the anterior cephalic appendages. That this had already taken place in its ancestry is indicated by the absence of the anterior glabellar furrow present in so many other trilobites, mostly the more ancient.

The writer's studies on the ontogenies of trilobites led him "to definite conclusions as to which characters are primitive, furnishing indeed the characters of the common ancestor" (Raw 1925, p. 309–10). To the 11 characters then mentioned and here abbreviated, others, at that time withheld, are here added, incorporated in Nos. 8, 10, 11 and 12.

1. Segments numerous.
2. Trilobation pronounced, body strongly divided into axial and pleural lobes.
3. Pleural lobes at least as narrow as the axial.
4. Proportionate length of each segment greater than in later trilobites.
5. All normal segments bearing a median spine.
6. Post-cephalic pleura truncated at their ends by rearward pointing spines.
7. Cephalon relatively long, the cheeks narrow, especially the free cheeks, bounded within by the facial sutures.
8. Rachis of cephalon composed dorsally of six segments similar to those of the thorax.
9. Cephalon bearing seven peripheral spines (heptacicephalic), one pair (parial) on the free cheeks, issuing from the midlength of the shield, another pair (procranidial) at the anterolateral angles of the cranidium, and a third pair (metacranidial) at the posterolateral angles of the same, the seventh being the occipital.
10. Eyes long, forming the inner boundary of the free cheeks, and joined by ocular ridges to the "anterior glabellar lobe" (i.e. to the anterior of five axial divisions of cephalon, or still more primitively between the first and the second of six), and extending rearward to the occipital segment.
11. Cephalon bearing ventrally: (1) a hypostome; (2) a rostrum under the space between the procranidial spines (or their loci), bounded by the anteromarginal suture in front, the hypostomal suture behind, and the connecting sutures at its ends—between it and the doublure of the free cheeks or their equivalent; (3) a pair of uniramous antennae issuing laterally on either side from cover by the front of the hypostome; and (4), behind this, so far as known, bearing only typical biramous trilobite appendages.
12. Pygidium small, with anal cerci (found only in *Neolenus*) and normal biramous appendages on the segments.

Considering how much more primitive are primitive trilobites than are any other arthropods Recent or fossil, the characters above enumerated together with other considerations discussed below reveal not only the morphology and phylogeny of the trilo-

bite class, but the origin even of the prot-arthropod; and by so doing they shed a flood of light, as the author believes, on the relation of the various arthropod classes.

8. THE EYES OF THE TRILOBITES

An extended treatment of the various eyes of trilobites would make this paper too long; and as they have such close relationships with those of all other arthropods, a discussion of this subject is withdrawn for later publication.

The eyes are of great morphological importance as has been stressed by Hanström. He claimed that only trilobites and xiphosures have three "pairs" of eyes (1926, p. 40) which he distributes in three visual spheres. Though he has been opposed by Johanssen (1933), Hanström's visual spheres are important realities, though badly named. But we can go further: here it may be claimed that the early Precambrian trilobites, more primitive than any known Cambrian form, inherited on their heads no less than four different classes of eyes, which were handed down to their descendants the chelicerates. All these four classes also are met with in known trilobites, but perhaps no known species exhibits them all.

Three of these classes of eyes were inherited from the polychaet, through the pro-arthropod, the prot-arthropod and the deut-arthropod, namely: Class I, two pairs of prostomial eyes, represented in some trilobites and still existing in a descendant as the dorsal median eyes of *Limulus*; Class II, a pair of eyes from the peristome which in the trilobite migrated on to the hypostome, being represented by the pair of maculae, and which are represented in *Limulus* by the so-called ventral eyes, and in Scorpiones as the median pair, and in some insects as a unique pair; Class III, six pairs of dorsal segmental eyes, which though poorly represented in trilobites appear still in the embryo of *Limulus* and in different form even in the adult; and also abundantly in larval insects.

Besides these nine pairs, inherited from the polychaet, the trilobite head also inherited from the immediate ancestor, the deut-arthropod—Class IV the compound or radiate eye, which was evolved within the arthropod, and distinguishes that stage from the prot-arthropod furnished only with simple eyes.

Nor were these ten pairs of cephalic eyes all that the trilobite may have inherited. In the eunicid polychaets segmental eyes occur throughout the body; and in the Asaphidae are Pander's organs, which often occur on the doublures of the pleura throughout the thorax. These closely resemble the maculae of primitive trilobites, which have been accepted as eyes. The point need not be discussed here; but they seem to be serially homologous with the eyes of classes II and III.

9. RELATIONSHIP OF THE ARTHROPOD TO THE POLYNOID POLYCHAET

Relationship of the arthropod with the ancestor of the Polynoidae has already been claimed above (3 and 5), because from their common ancestry are derived not only polychaet but even polynoid characteristics in the arthropod. Among the annelidan features mentioned the periodicity in segment type and appendage type has its counterpart among annelids only in that family. For this the writer here suggests the term merocyclism. Then in 5 it is suggested that the extent of the arthropod head was determined by the body of the ancestral polychaet as it ceased its pelagic life and settled on the sea floor. The segmentation of this larva hints that it too may have been determined by merocyclism; a principle, which, it is suggested below, offers the only explanation of the tagmatism and nomomerism characteristic of so many arthropods.

In this polychaet family the incidence of the elytra (scale-like modifications of part of the notopodium) is on the 1st normal segment (1st behind the peristome), on the 3rd and 4th, the 6th, and thereafter on alternate segments. In the subfamily Acoetina this same incidence continues; but in the Hermionina and Polynoina, after the 22nd normal segment it is on every 3rd; in the Sigalionina after the 26th it is on every segment.

In trilobites we have a closely comparable phenomenon. The writer has claimed as primitive in the trilobite head, the presence of three pairs of lateral cheek spines, marking specialised segments "macrosomites." They occur in *Olenelloides*, in larval

stages of *Olenellus* and *Leptoplastus* and in other forms (Raw, 1952); and their homologues can be widely recognised. Primitively they lie at the anterior and posterior corners and laterally at the midlength of the shield; and if we suppose that each one of the middle pair is a coalescence of two adjoining spines on normal segments 3 and 4, the incidence coincides exactly with that of the elytra in the Polynoidae namely on normal segments 1, 3 and 4, and 6; thus the head ends with a macrosomite (Raw, 1925, p. 232). Behind the head, however, in some Olenellidae we have the incidence of macropleura with pleural spines on each 3rd segment, which is the same as that of the elytra in Hermionina and Polynoina behind the 22nd segment. In some malacostracan orders, especially Stomatopoda, Isopoda and Amphipoda we tend to have a change of appendage type every third segment, also representing this ancestral periodicity. The tagmatism and nomomerism in the arthropods is also by the writer referred to the same origin. The macrosomites seem to have been specialised in a variety of ways: by larger size, by larger pleura or appendages or axial spine; probably in all these ways. Changes of tagma occur at the macrosomites; and the body of many nomomeristic arthropods—Insecta, Malacostraca and the long-bodied Arachnida—had their effective termination originally at the 15th segment behind the head, the 5th post-cephalic macrosomite; behind which the remaining segments extensively aborted. In the long Arachnida, i.e., Eurypterida and Scorpionida, the writer believes the termination was effected by the dorsal spine of the segment, as is certainly the case in *Olenellus*. In *Limulus*, however, it was terminated on the 9th, also a macrosomite. In the crustacean and the insect it was not the dorsal spine, but some other much-used part of the 15th segment which was the determining factor.

The limitation to these comparisons between the trilobite and the polynoid should here be specified. Merocyclism in the trilobite is a slender thread; but the way in which it interprets the trilobite and other arthropods gives it great importance. The application of merocyclism to the head of the trilobite has already been given. Behind the head it is best exhibited by *Olenelloides*, a small form which only exhibits two cycles

⇒

FIGS. *3A–H*—Trilobites with primitive characters; all, as found, flattened by sedimentation in shale. Visual surface of eye not seen: it coincides with the ocular section of the facial suture (the outer limit of the eye lobe) and in life would extend vertically beneath this.

3A–F are primitive by their narrow pleural lobes, their relatively long segments and unreduced head rachis, their retention of pleural and axial spines and of merocyclism (Sec. 11, h). Except in paucity of segments they resemble the ancestor (the deut-arthropod).

G is a reversion from an *Olenellus* with a semi-ovoid body form.

The pleural spines of macrosomites are numbered counting the first dorsal segment as 1. In all figures: a = procranidial spine, b = parial, and c = metacranidial.

In *A*, *B*, *F* and *G* the anterior glabella lobe = 2 segments.

3A—Leptoplastus salteri (Callaway). Basal Ordovician (upper Tremadoc). Heptacicephalic larval olenid in Meraspid Degree 3, with specialised anterior eye. (Raw, 1925, p. 249).

3B—Olenelloides armatus Peach. Lower Cambrian. An adult though small, heptacicephalic olenellid. Head specialised by loss of suture and by forward eyes; probably a reversion in respect of cephalic spines. Thorax with macropleural macrosomites as on the head (Peach, 1894, pl. 32).

3C—Albertella helena Walcott. Middle Cambrian. With macropleural spines on macrosomites (Walcott, 1908, pl. 2, fig. 1, corrected by fig. 5; also 1917, pl. 7, fig. 4, corrected by figs. 1 and 2).

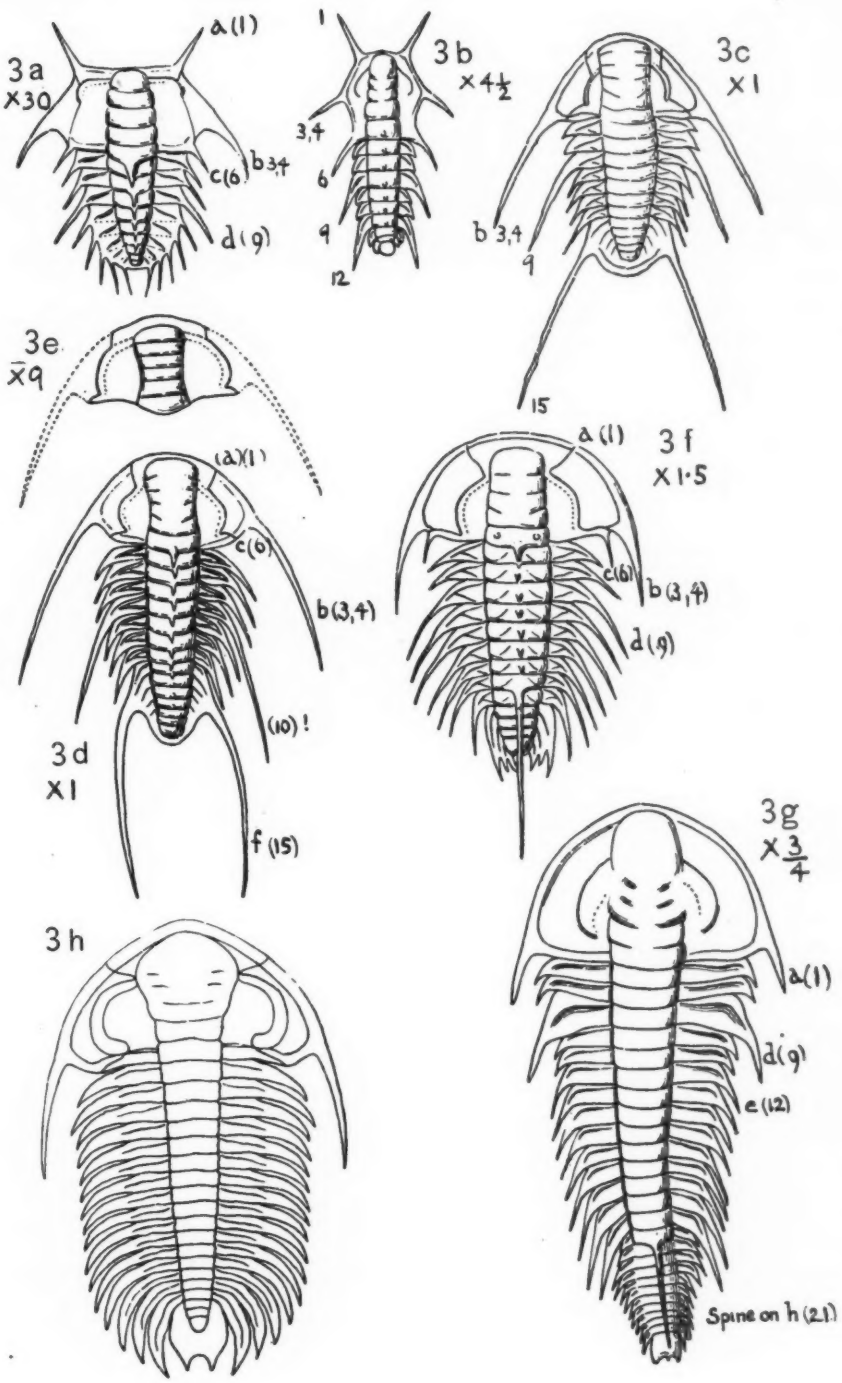
3D—Albertella bosworthi Walcott. Middle Cambrian. More primitive than *C* in longer eye, the position of the parial spines and in the retention of axial spines; but the 10th segment is macropleural! (Walcott, 1917, pl. 7, figs. 3, 3a.)

3E—Larval cranidium of the last named. Primitive in rachis and in course of facial suture (Walcott, 1917, pl. 7, fig. 3d).

3F—Zacanthoides typicalis Walcott. Middle Cambrian. Note its retention of metacranidial spines and long eye (Walcott, 1886, pl. 25).

3G—Olenellus vermontanus (Hall). Lower Cambrian. Head specialised by rearward revolution of the procranidial spines as well as parial, and by loss of facial suture. Thorax exhibits secondary even development of pleura behind the 6th post-cephalic segment (Walcott, 1910, pl. 26).

3H—Paradoxides rugulosus Corda. Middle Cambrian. Primitive example with long eye and the primitive semi-ovoid body form (Raw 1927, fig. 15, p. 132).


3a
×30
a(1)
c(6)
b3,4
d(9)
1
3,4
6
9
12
3b
×4½
3c
×1
b3,4
9
15
3e
×9
(a)(1)
c(6)
b(3,4)
3d
×1
(10)!
f(15)
a(1)
3f
×1·5
c(6)
b(3,4)
d(9)
3g
×¾
a(1)
d(9)
e(12)
Spine on h(2,1)
3h

by macropleura on the third and sixth segments (Peach, 1894, pp. 671–4; Walcott, 1910, pl. 40). In *Olenellus* and *Paedumias* segment 3 is a macrosomite and also frequently is segment 6 as in *O. vermontana* (l.c., pl. 26); *O. thompsoni* (l.c., pl. 33 called "*P. transitans*") and *P. transitans* (l.c., pl. 34, fig. 2). But in all these, supersession of this feature by lengthening and graded pleura has set in, and there is no trace of it behind except for the axial spine on segment 15 behind the head in *Olenellus*, *Paedumias* and *Wanneria*. Within this same family complete supersession has already occurred in *Nevadia*, *Elliptocephala*, *Holmia* and *Callavia*.

In most other families, though we have macrosomites marked by macropleura or by great axial spines, there is little system to be observed. In Paradoxidae it is the second not the third, that is often a macrosomite. In *Albertella helena* it is the third segment, which is macropleural; in *A. bosworthi* it is the fourth; in both forms there is another macropleural segment on the pygidium which is perhaps six segments beyond (Walcott, 1908, pls. 1, 2). In the known history of the trilobites evident merocyclism early died out, being almost limited to Cambrian forms: it is because of their especially primitive character that we see it here, for their mode of life by the adoption of a semi-ovoid body-form led to its suppression.

It is not suggested that the annelid ancestor of the arthropods was at all closely comparable with the *modern* polynoid. The arthropod originated very long before Cambrian time, possibly as long before, as the time that has elapsed since. The modern polynoid is highly specialised in its brain, as well as in its appendages, but the annelid ancestor of the arthropod was primitive, with very much less specialisation in both these respects. Indeed, careful comparisons between polychaets and arthropods suggest that the polychaet ancestor of the latter combined in itself characteristics of Eunicidae, Phyllodocidae and Polynoidae.

Regarding the origin of the peculiar incidence of the elytra on the anterior segments of the last named, the writer has shown that the brain of the polychaet is highly compound, and that as a result of its aggregation the segments which lie immediately behind the prostomium were originally much further back on the body. The limitation of merocyclism to the Polynoidae among polychaets suggests that it may not have been a characteristic of the primitive polychaet, but that it originated in this family. If so, the polynoid originated the arthropod. The fact that from the 4th segment behind the peristome the elytra are on alternate segments back to the 22nd in all subfamilies, suggests that primitively the same alternation may have extended right to the front, and also to the rear; i.e. in what is now the head of the arthropod, as now, on the 6th and 4th normal segment, but then on the 2nd and lastly on the peristome. If later there was a transference of function rearward by one segment in the case of the first two macrosomites, we should get the state of things now existing in the family.

All of this comparison between the polynoid and the arthropod classes—Trilobita, Arachnida, Crustacea, Insecta; and the bearing of merocyclism on tagmatism and nomomerism were already in the writer's mind, and had been written down at much greater length than in the above outline already before 1922, when they were submitted to the late Prof. F. W. Gamble, who looked forward to their publication.

The author's claim in 1925 that the head spines of trilobites included three different pairs and that they were important morphological entities (l.c. pp. 232, 310, etc.) was opposed by Swinnerton (l.c. p. 322). The claim was repeated in 1927, 1936, and 1937 and was opposed by Raymond (1928, p. 168); but this claim of relationship with merocyclism has never before been published. The claim of Swinnerton that the spines are merely coenogenetic adaptations to the pelagic life of the larva, and that of Raymond that the origin of the spines is "mechanical" cannot stand in face of the comparison with the polynoid which furnishes a basis in merocyclism for the development of the spines in those particular places. Recently Ross (1951) has furnished very strong supporting evidence, the significance of which has been discussed (Raw, 1952).

10. THE SUTURES AND EYES IN TRILOBITES: THEIR RELATIONSHIPS AND ORIGIN

Figures 4, A–I

A highly characteristic, indeed, a unique feature of the trilobite head is the definite system of soft sutures between the strengthened parts—the cranidium, rostrum, hypostome and free cheeks. It is generally believed that the "dorsal facial sutures" are connected in origin with the compound eyes. We will consider therefore here the evolution of sutures and of eyes. In the most primitive forms the dorsal facial sutures divide the dorsum into a median cranidium (consisting of axial lobe and fixed cheeks) and the free cheeks bearing the compound eyes. Each dorsal facial suture consists of a middle section past the eye (the ocular section—running near to the inner boundary of the visual surface), and anterior and posterior branches, which run outward to cut the margin of the head, and ventrally are continued as the "connecting sutures" across the doublure. On the ventrum the hypostome is separated in front, by the "hypostomal suture" from the rostrum (the anterior part of the doublure), which, in turn, is separated from the dorsum by the "rostral suture," whereas at the sides the "connecting sutures" separate the rostrum from the rest of the doublure.

As to the origin and significance of the sutures, past writers agree in regarding the free cheeks as the pleura of a segment, a theory which the writer strongly opposes; but whereas one group make them the pleura of a ventral segment represented by the rostrum; the other associates them with the anterior dorsal segment. In this case the anterior branch of the dorsal facial suture is presumably secondarily developed for ecdysis; for all agree that the function of the sutures is to liberate the head in that operation.

The writer's view differs entirely from these as to the distribution of the segments, and to a large extent as to the origin of the sutures, especially of the part past the eyes. *All* the sutures, the writer believes, originated either in the soft joints between the strengthened terga of the anterior segments, or the gaps between the pleura of the proarthropod; *except* for the ocular sections past the eyes. These last originated in the two lines of thin cuticle over the six segmental eyes on each side, belonging to the segments that were to form the head of the arthropod.

In detail: the hypostomal suture was the joint between the prostomial tergum and the peristomial; the rostral suture was between the terga of the peristomium and of the first normal segment; the anterior branches of the dorsal facial sutures were the gaps behind the pleura of the first normal segment, and the posterior branches of the same were those in front of the pleura of the sixth or last head segment.

Some have regarded the preglabellar field, when present, as a segment; but this is quite absent in the most primitive forms, where there is nothing between the glabella and the rostrum except a very narrow roll—a stiffening of the head margin.

In the writer's view the preglabellar field must be regarded as an adaptational excresence. In the ontogeny of *Paradoxides rugulosus* and some other long-eyed species, it is quite absent in the earliest stages, and later develops greatly, only to be again reduced when the glabella expands (Raw, 1925, pp. 275–6).

That the part past the eye had the origin mentioned is suggested by the following considerations. Segmental eyes are best developed in the errant polychaet suborder Eunicimorpha, which the writer has claimed as the most primitive (1949). In *Eunice*, the eyes, indicated by black spots, occur on the lateral edges of the terga at the base of the appendages; and they lie along straight longitudinal lines. But in the prot-arthropod they must have occurred on the pleura, as *Limulus* and the trilobite show (indicated by *Phacops*, *Harpes*, *Trinucleus*, and suggested by Pander's organs); and we can therefore assume that these eyes formed two straight lines along the body of the proarthropod crossing the pleura.

The foremost pair of segmental eyes has been claimed above as having lain on the peristome, and as being the pair represented by the ventral eyes of the larval *Limulus;* which Hanström has homologised with the hypostomal eyes of the trilobites. Though these eyes in *Limulus* are covered with a thin cuticular lens (Hanström 1926, p. 28),

in the primitive Paradoxidae and Olenellidae (Middle and Lower Cambrian respectively) they are represented in the fossils by holes through the test; a fact which indicates that the cuticle covering them was thin and uncalcified.

After the "subretroversion" which carried both the prostomial and peristomial eyes beneath the body, the eyes of the anterior dorsal segments would become for many purposes the most important ones. Consequently they might be expected to increase in size, while owing to the continuance of subretroversion the pleura as far back as the macrosomite, normal segment 6, coalesced outwards from the body in the formation of the head. After the coalescence of the pleura the various soft joints of the head became strengthened or ankylosed, except so far as this was controlled by the need for ecdysis. The enlarged eyes covered with soft cuticle formed now a new continuous zone of weakness from front to rear across each cheek, additional to the old intersegmental divisions. But the head comprised among its segments four macrosomites, viz: normal segments 1, 3 and 4 and 6, which differed from the rest by having longer pleural spines. If after the coalescence of the pleura the spines also on the adjoining segments 3 and 4 also coalesced, we should have the condition exhibited by the forms most primitive in this respect (*Olenelloides* and larval forms within the Olenellidae, and *Leptoplastus* among the Olenidae). These bear three pairs of spines in addition to the occipital, and so are "heptacicephalic" (Raw, 1925, pp. 242–6, 306–8; 1927, pp. 11–14, 24–28 etc.); and they were claimed as indicating this heptacicephalic ancestor for the trilobites. The anterior pair of spines, the procranidial, are directed forward and

→

FIGS. 4*A–I*—Types of cephalon in primitive trilobites showing disposition of homologous parts.

Of the head spines primitively present, as seen in *A*, the semi-ovoid body-form favoured the retention of one pair only at the posterolateral angles.

But these may be the metacranidial, primitively in that position—proparial trilobites—Figs. *B* & *C;* or the parial, rotated to the rear—mesoparial trilobites—Figs. *D* & *E;* or the procranidial may also be revolved to the rear, as in the metaparial—Figs. *F, G, H*. This involved the carriage also of the connecting sutures RS to a position beneath the genal angle, and the stretching of the rostral suture RRR into a semicircle. As these were not sufficient for ecdysis, the dorsal facial sutures XO_1O_2X are ankylosed; and only the rostral and connectives remain.

A = procranidial spine, B = parial, C = metacranidial.

HHH = hypostomal suture, RRR = rostral suture, RS = connecting sutures. RO_1O_2Z = dorsal facial suture of each side, comprising anterior branch, ocular section and posterior branch. In primitive trilobites the ocular section coincides with the dorsal boundary of the eye.

4A—Heptacicephalic larva of *Leptoplastus salteri* in Degree 1, with transitory pygidium. The head spines all retain original positions.

4B—The proparial *Dalmanitina hausmanni* Brogn., dorsum; with great development of metacranidial spines in their original position.

4C—The same; ventrum. Note how the median parts of pairs of appendages must have worked dorsad of the hypostome. The connecting sutures are ankylosed.

4D—The mesoparial *Paradoxides spinosus* Boeck, dorsum. The parial spines have moved rearward.

4E—The same; ventrum. The hypostomal suture is here ankylosed, but not in all species of the genus.

4F—The metaparial *Callavia callavei* (Lapworth), dorsum. Procranidial and parial have both moved rearward to the posterior border, and have coalesced in the genal spine. The intergenal spine is the metacranidial. This, from calcareous sandstone, is preserved with full relief.

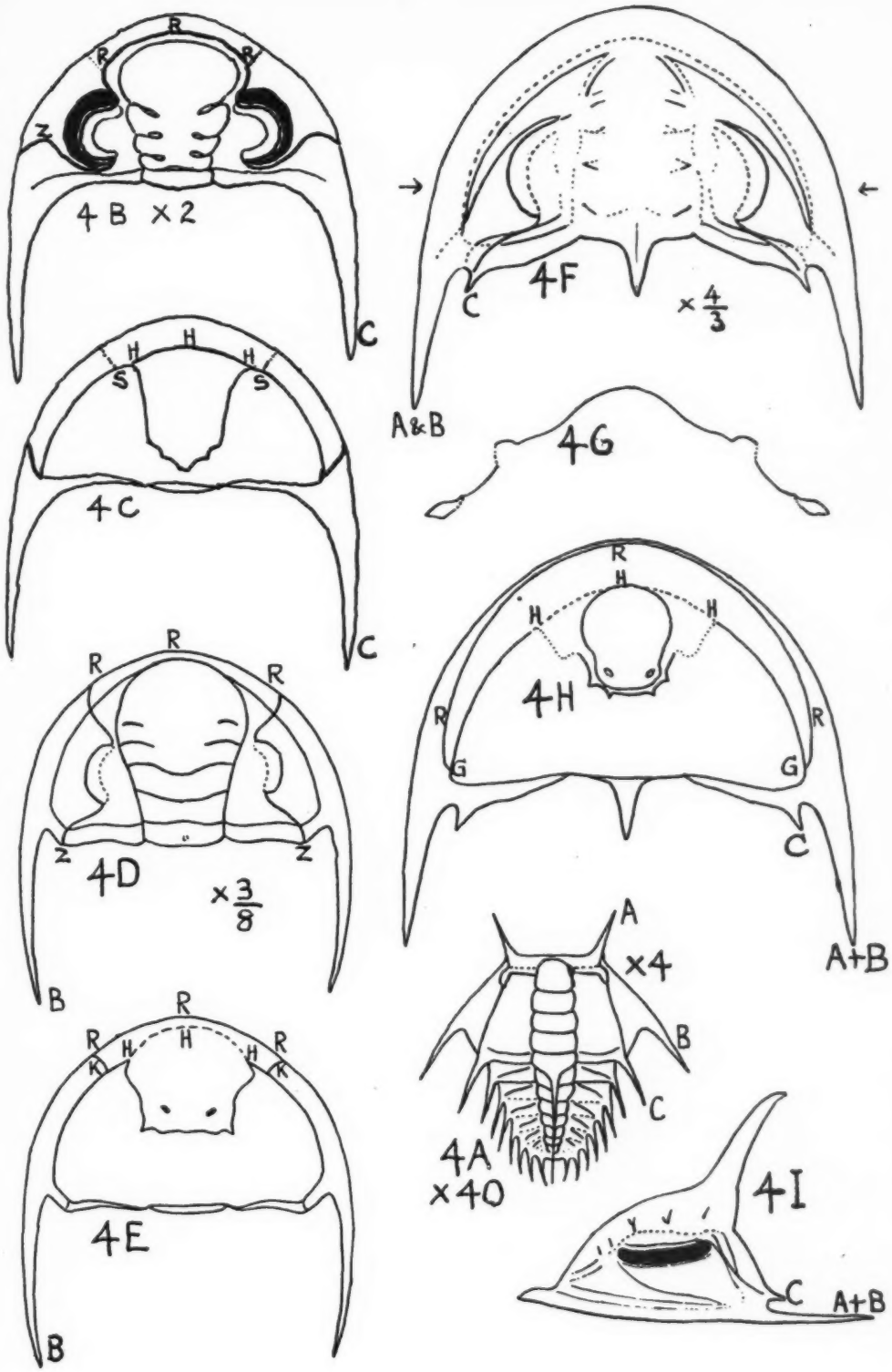
4G—Cross section of same along line of arrows. The dotted line represents visual surface of eye.

4H—The same, ventrum. Note so-called "marginal" suture, which is the semicircular rostral RRR with the connecting suture RS at each end. The hypostomal suture, as in E, is ankylosed.

4I—Lateral view of same.

The vestiges of the anterior and posterior branches of the dorsal facial sutures, very clear in *Holmia* and *Kjerulfia* as well as *Callavia*, are represented in Figs. *F* and *I* as continuous lines— the anterior branch from O_1 outward and rearward to the inner edge of the border, the posterior from O_2 to Z. This touches another line which is the pleural ridge of the occipital segment, and both cross the marginal furrow.

A, F, G, H, I, original; reproduced from Raw 1937, figs. 1, 4, 5, 6, 7. *B, C, D, E*, after Barrande, redrawn from Raw 1925, pl. 15, and Raw 1937, p. 581.


R
R
R
Z
4B ×2
C
H
H
H
S
S
4C
C
R
R
R
Z
Z
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×3/8
B
R
R
H
H
H
R
K
K
4E
B
→
←
C
4F
×4/3
A&B
4G
R
H
H
H
R
R
G
G
4H
C
A+B
A
×4
B
C
4A
×40
4I
C
A+B

outward, the others outward and rearward, but the parial most outward and the metacranidial most rearward. The necessity of releasing these pleural spines in ecdysis was, the writer believes, the most important factor in the retention of the particular lines of soft cuticle which have become the dorsal facial sutures. Motion of the now soft body forward and rearward within the old shell would release it from the metacranidial and procranidial spines respectively, but for release from the parial the free cheek fell away by a parting along the line of eyes combined with partings along the intersegmental divisions at each end; for after the coalescence of the pleura the line of eyes began to shorten and so retreated from the original positions of the first and last pleura, as is indicated by the trilobites.

In several olenellids, e.g., *Elliptocephala asaphoides*, *Olenellus gilberti*, *Kjerulfia lata* as well as several *Paradoxides*, e.g., *P. rugulosus*, the eyes extend past four glabella segments, and this is the case in very many less well known forms in other Cambrian families. Also in many primitive Cambrian forms it is an observed fact that in the ontogeny, the palpebral lobe, which indicates the length of the compound eye, is at first long, equal in length to four glabella lobes, i.e. four segments, whereas in the adults it is shorter. Also in the young it is less curved. The same kinds of change characterise also the succession of adults in various families in the course of geological time. Hence we can infer that the eye in Precambrian time was longer and straighter in all families (1925, pp. 275–8, *Paradoxides bohemicus* and *P. spinosus;* 1927, pp. 132 and 134, figs. 12–21).

In a head of the convexity imposed by the subretroversion there would be an obvious advantage in the lines of eyes changing from straight to outwardly convex, so that they were directed all round, as befitted a slow animal. Also, two other great changes followed—I, changes in the nervous system, and II, the evolution of the compound eye.

The segmental eyes would originally be innervated each from its own ganglion of the "lateral" chains, which were to become the ventral chain. But the compound eyes of the arthropod are each innervated by a single nerve. Also in primitive trilobites each eye-lobe is connected, but only in front, and by an eye-ridge with the glabella. This suggests that the eyes, after the coalescence of the pleura, secondarily became innervated by the nerve of the foremost, probably belonging to the 1st normal segment. Where six dorsal segments are indicated, as in *Zacanthoides*, *Paradoxides* and others, the ocular ridge joins the glabella at the junction between the first and second. Where only five are indicated, the anterior glabellar lobe is a coalescence of the two, and in this case primitively the ocular ridge is directed towards its mid-length.

But in the Lower or Middle Cambrian *Bigotina bivallata* Cobbold, of the Carteret region, N. W. France, Cobbold (1935, p. p. 385 and pl. 13) has described and figured the ocular ridge as dividing into two before reaching the glabella, thus suggesting the specific name. This reminds one of a peculiarity of the Olenellidae, where in *Holmia*, *Kjerulfia*, and in several species of *Olenellus* and *Paedumias* the ocular ridge and palpebral lobe is double throughout, with a narrow furrow between two ridges. These facts suggest that the posterior eyes of the head were all connected together by a nerve and were innervated by the nerve of the second pair before they joined the first. Is the inner ridge connected with the earlier line of simple eyes, and the outer with the later compound eye? It may be noted that the simple eyes are almost absent from trilobites and that in later forms the palpebral lobe is simple.

As to the morphological significance of the ocular ridges connecting the palpebral lobes with the glabella, the writer suggests that they are homologous with the pleural ridges of the thoracic segments and with the pleural ridges of the fixed cheeks of protaspids of Olenellidae, Paradoxidae and Olenidae already mentioned in Section 4 which are just behind them. But the ocular ridge was greater because it housed the important optic nerve and the accompanying blood vessel.

But the brain already dealt with the sense of sight, and after the subretroversion, when it occupied the labrum, there was a tendency for the brain as well as the prostomial eyes to migrate forward, as well as up to the light. In this way, largely due to the migra-

tion of the brain, the nerves of the "ventral" (peristomial or rostral) eyes and those of the anterior dorsal eyes would secondarily secure direct connection with the brain. This may have preceded the common innervation of the dorsal segmental eyes by the nerve of the first. *Thus finally all the lateral eyes, ventral, dorsal and the compound, that was to follow, came to be innervated by the lateral optic lobes of the brain.*

The labrum which originally in the prot-arthropod would hold the brain is in the higher arthropods not even innervated by it, but by a part of the nerve chain to the rear. *This innervation, we can be sure, is secondary.* The great importance of the eyes in these has caused the brain to be drawn to them and away from the labrum: the oesophageal connectives which primitively in the arthropod ran down and rearward to the brain, now in these extend forward and up to it. But in *Limulus*, which has retained a trilobite body-form, the brain is still a little below the level of the ventral chain. In *Scorpio* it is above the level: in Crustacea and insects it is high above.

A possible mode of origin of the compound eye is strongly suggested by the trilobite. The prot-arthropod has above been furnished on each side of the head with an outwardly bowing crescentic line of simple eyes covered with thin cuticle, which last was to become part of the dorsal facial suture of the trilobite. These eyes were innervated by a corresponding line of optic nerve, following the same route and reaching the brain via that of the foremost. The compound eye of the trilobite is situated on the free cheek or its homologue, just outside the line of suture, i.e., the line of the lateral eyes and optic nerve. Now an areolar surface-pattern is very frequent in trilobites—a network of raised ridges enclosing depressed polygonal spaces. It characterises the Olenellidae, Paradoxidae, Cryptolithidae, and occurs in several other trilobite families; and it is also met with in ancient Crustacea—*Dictyocaris* (Störmer, 1935, pl. 1, fig. 2, pls. 2, 3) and in *Anaspides*, one of the most primitive Malacostraca (Hanström, 1934, p. 7, fig. 5a). The scale of this pattern is often very minute: in *Dictyocaris* and in trilobites it measures 4 (or even 6) meshes to 1 mm. Let a light shine through the conical surface of skin with this fine pattern of opaque ridges surrounding transparent spaces beneath the crescentic line of eyes, and it imprints itself, through those which are in the right position, on the light-sensitive nervous mass inside. From such a simple beginning it is possible to picture the evolution of the radiate subspherical eye with all its refinements.

The above deduced derivation of the arthropod eyes gains strong support from the ontogeny of *Limulus*. According both to Patten and to Kingsley, before the development of the compound eye, a nerve from the optic ganglion of each side is connected with the segmental sensory organ or eye in each of the six limb-bearing segments. These segmental "eyes" are here claimed to be represented by the pigmented body beneath the retina (Patten, 1889) or the "rudimentary compound eye" (Demoll, 1914) submerged beneath the compound eye of the adult.

According to Patten and Redenbaugh (1900) the optic nerve of the compound eye arises from the dorsal side of the brain just in front of haemal nerve 1, or the lateral nerve, i.e. the dorsal tegumentary nerve of the cheliceral segment; and follows closely the course of this nerve. Both proceed round and in front of the muscles moving the second pair of appendages, and then extend back to the eye. This may be taken to indicate that the innervation of the compound eye and so also the dorsal segmental eyes in the ancestor of *Limulus* was via the pleuron of the cheliceral segment i.e., the first glabella segment of the trilobite and so presumably proceeded originally from the ganglion of that segment.

These changes in the nervous system, made possible by the coalescence, would be accompanied by correspondingly great changes in the circulatory system, for to quote Lankester (1910 A, p. 294): "a very remarkable feature in *Limulus* first described by Owen is the close accompaniment of the prosomatic nerve centres and nerves by arteries; so close indeed that the great ganglion mass and its outrunning nerves are actually sunk in, or invested by arteries." The changes in nervous and circulatory systems which have occurred in the ancestry of *Limulus* within the pleural "lobes" of the

body can be read in its anatomy; and it is extremely probable that those of the prosoma already existed in the trilobite. The eye-line for example probably housed both nerve and artery, the hepatic artery from the occipital segment enclosing from the eye onward the lateral eye nerve, besides continuing outward to form a marginal artery. In *Limulus* with the coalescence also of the abdominal pleura we have also a posterior marginal artery (Milne Edwards, 1873).

After the evolution of such a long narrow crescentic compound eye, as is seen in some Olenellidae, Paradoxidae, Zacanthoidae, and many others, in several lines the eyes became concentrated, changing to a short arc or to some approach to a hemisphere. In all these cases the suture still continued to coincide with the median side of the eye; but the concentration involved changes in both the anterior and the posterior branches of the facial suture. Apart from this the sutures have submitted to marked evolutions in various other ways, especially in correlation with the suppressions and migrations of the three pairs of cheek spines, which evolutions determined the types of head shield called proparial, mesoparial, and metaparial (Raw, 1925, pp. 310–312, pl. 15; 1927, pp. 10–14). In the last named the dorsal facial sutures disappeared by ankylosis. Another cause of modification in the suture was the loss of function by the compound eye. In trilobites thus affected, the dorsal facial suture has, in some, migrated towards the margin (Conocoryphidae, Raphiophoridae), and, in others, has in some way (most probably in the same way, or else as in the metaparial olenellid) been replaced by a truly marginal suture. On the ventral side, too, the sutures suffered marked evolution: sutures may be lost by ankylosis, e.g., the hypostomal in Paradoxidae and Olenellidae; sutures may be extended, e.g., the rostral suture in the Olenellidae extended to the genal angle; or sutures may migrate, as the connecting sutures, bounding the rostrum at its ends, in the same family; but in the Olenidae, Asaphidae and their allies the connecting sutures have migrated in the opposite direction, i.e. to the mid-line, and there suffer union or even ankylosis. Further, almost all stages in this process can be seen, sometimes different stages can be seen within the same family, e.g. Asaphidae. With such a mode of origin of the facial sutures, arising as claimed above even in the protarthropod and inherited by the trilobite, it is obvious that all facial sutures properly so called are here homologised with one another. Swinnerton, however (1919), claimed that they had arisen independently in several distinct lines of descent, and that only his ventral suture seen in the Olenellidae was primitive, on which he based his order "Protoparia," which has since been shown to be secondary.

The sutures were retained to facilitate ecdysis. What were not required for this ceased to be used, and so were lost, e.g.: the connecting sutures in the Phacopidae; or the whole of the dorsal facial suture in the Olenellidae, which were superseded by the extended rostral suture and connecting sutures on the ventrum.

The writer showed in 1925 and supported it fully in 1936 and 1937 how as indicated by characteristics of the genera *Holmia*, *Callavia*, and *Kjerulfia* the Olenellidae had lost the dorsal facial sutures, and had secondarily acquired a marginal suture by the extension of the rostral suture to the genal angles. This was brought about by the migration of the procranidial spines with the connecting sutures also round to the genal angles (1925, pp. 301–5; 1936, pp. 239–263; 1937, 578–587) and was indicated by comparison of the characteristics of those and other genera of Olenellids with *Paradoxides*. It was claimed also that an ancestor of the latter (mesoparial, but retaining still the procranidials) had given rise to the metaparial Olenellidae (1927, p. 140; 1937, pp. 594–6). This has been too much for those who do not realise the extreme incompleteness of the geological record. Swinnerton who made pleura appear first in the trilobites, and instituted his order "Protoparia" to receive "Trilobites and Trilobite-like organisms in which the absence of facial sutures is primary," though including in it at first only the Marellidae (1915, pp. 493, 542), later (1919) made it an ordinal name for the Olenellidae claiming that they were primitively without facial sutures. He secures a faithful disciple in Störmer (1941) who claims the marginal suture of the Olenellidae as the parent of all sutures; and

claims the descent of all the orders from creatures like the protaspids of *Elliptocephala* and *Holmia*. From the "Protoparia" arose directly the trinucleid "Hypoparia" and the proparian trilobites, and from the latter branch, the mesoparians. He supports himself in this by claiming that the protaspids of *Dalmanitina* and *Olenus* have marginal sutures; but for this there is no evidence whatever (l.c., p. 149; see Raw 1952). He makes much of the retarded development of his "pre-antennal" segment, but does not connect it with the position of the hypostome below (l.c., pp. 153, 158).

The evolution of sutures and of eyes discussed above suggests a solution of the old problem as to the origin and significance of the moveable eye-stalks so frequent in the Crustacea: "How did they originate and are they appendages?"

The eye-stalk may well be a development of the free cheek bearing the eye, become moveable. The free cheek is part of four coalesced pleura, which were appendages of the pro-arthropod; and the eye is a modification of the common nerve of six segmental eyes borne on those pleura. These particular parts of the appendages are further believed to be the morphological equivalent of the dorsal cirrus of the polychaet. This may help to explain why "the stalked eye of Decapods, when excised with its peripheral ganglion, can regenerate in the form of an antenna" (after Herbst in Smith, G. 1909, p. 6).

Besides the many new claims made in this paper the author reiterates with confidence that both the various parts of the cephalic sutures, and the seven spines of the heptacicephalic ancestor (indicated by Olenellidae, the larval stages of *Leptoplastus* and less completely by other forms) are important morphological entities. He also claims again the procranidial spine as the pleural spine of the first dorsal segment; the parial or free cheek spine as the coalesced pleural spines of the third and fourth segments; and the metacranidial spine as the pleural spine of the sixth or last; and that these three pairs longest survived the coalescence, because just those segments were the macrosomites with the largest spines; and that these as well as the occipital spine were inherited from the pro-arthropod.

The procranidial spines, primitively projecting in front, are in general lost: they were retained by the larva of *Leptoplastus* (and probably other Olenidae) doubtless for flotation, in adaptation to its pelagic life; and they seem to be represented also in *Telephus*, an aberrant genus with enormous eyes and parial spines, which may well have been pelagic in the adult. Their retention by the Olenellidae as the genal spines is attributable to their rotation to the rear in adaptation to their early settlement on the sea floor. Their existence in primitive Ordovician trilobites in early stages has however lately been demonstrated (Ross, 1951, interpreted by Raw; 1952).

11. THE CEPHALIC APPENDAGES IN TRILOBITES: THEIR NUMBER AND THEIR ALLOCATION

There is a large literature on the limbs of trilobites, to which the student must be referred. All that will be added here is a short criticism of it, and the writer's own conclusions.

Usually the limbs are not preserved at all, which can be attributed to the perishable nature of their thin and relatively uncalcified cuticle. When they are, it must have been due, it is supposed, to poisonous conditions locally existing on the sea floor, which prevented micro-organisms from consuming them. When preserved, it is either in limestone, where they often exhibit full relief, but can only be realised with difficulty by sections; or it is in shale, where they are replaced by iron sulphide as iron pyrites, with some measure of relief, or they are carbonised and are exhibited as an extremely thin film (Walcott 1918, pp. 119–21).

The appendages of the head, where known, comprise a pair of uniramous antennae, and an uncertain number of pairs, Walcott and Beecher said four, of biramous appendages very similar to those of the postcephalic segments. These biramous limbs occur on all the segments of the thorax and also, where known, and without any great change over the pygidium, ending perhaps on the preanal segment; but in *Neolenus* (Middle Cambrian) there is, besides, a pair of antenniform appendages at the end of the body, presumably on the anal segment or telson.

The allocation of the antennae is a difficult problem. They are perhaps universally homologised with the similar organs in insects and the myriapod classes and also with the first antennae or antennules of Crustacea. Hence their position in the trilobite, the most primitive class, may indicate their position in the others. But in this they have already been assigned to four different positions. If they were derived from the prostomium of the polychaet this on our theory would mean that they belong to the hypostome: at the other extreme Störmer following Beecher, Raymond and others assigns them to the fourth segment in front of the occipital which, if we call the peristome a segment, is three segments to the rear. Others again have assigned them to each of the segments between.

Being so entirely different from other known appendages of the head, all of which are in trilobites so primitive, it is extremely improbable that the antennae belong to any of the normal segments. This would assign them either to the rostrum or the hypostome. They are represented by Beecher, Walcott and Raymond as arising from the ventral surface on either side of the hypostome, and by Störmer (1951, p. 112) as issuing from vertical body walls joining the hypostome with the glabella; but it is clear that on the contrary they emerged laterally from beneath it, for rounded notches for them indent the lateral margins when viewed from the side. The smooth sockets through which they emerged show often a very strong curvature from outward round to forward and sometimes beyond, suggesting that these antennae often left the protection of the head shield near together in front, as seen in *Triarthrus*. The sockets are well exhibited by the Asaphidae, Bronteidae, Illaenidae and Cheiruridae (Brögger 1886; Lindström 1900). Their form in cross section shows that they gave issue only to *a single* pair of appendages; and their curvature suggests that these were highly flexible, and therefore antennae. The fact that the side of the hypostome and its doublure were free of the antennae but moulded upon them rather suggests that the antennae do not belong to the hypostome: if they did one might expect them to arise directly from its side. The conclusion is inevitable that the antennae belong to the rostrum. Further, if we are to homologise the trilobite antennae with similar organs in modern arthropods, we can support ourselves by the conclusion of zoologists that antennae do not belong to the primitive arthropod brain innervating the eyes, and therefore do not belong to the hypostome which primitively housed this. Modern antennae are attributed to the deutocerebrum.

On this allocation, the antennae of the arthropod are inherited, not from the tentacles of the prostomium of the polychaet, but from the tentacular cirri of the peristome, which are exhibited in modern forms by most families including the Aphroditidae and Phyllodocidae. This conclusion, forced upon us by the facts, is comparable with those drawn from study of the polychaet. In the evolution of this the mouth lips were supplemented and extensively replaced in function by a succession of cirri from segments behind, cirri which became the palps and tentacles of the head (Raw 1949). Now in the evolution of the arthropod those tentacles of the head are lost, being replaced in function by the cirri of the following segment. In the subretroversion which originated the arthropod the bases of the appendages of the segments which became the head except for their pleura became enclosed in the cephalic fold. This explains the curious emergence of the antennae from under cover of the hypostome. In the subsequent evolution of the modern arthropod classes, whereas the Trilobites were relatively conservative, and the Arachnida lost the antennae entirely (though many zoologists homologise the chelicerae with them! e.g. Borradaile, 1935), in the other classes the antennae have extensively migrated, and have thus escaped from the enclosure.

The arthropod inherited its primitive mouth from the peristome of the annelid, which is represented as regards its tergum by the rostrum of the trilobite. Primitively in the arthropod and probably still in primitive trilobites the antennae were attached on either side of this mouth. Behind these antennae were the six pairs of appendages belonging to the six dorsal head segments: on this view therefore the mouth and antennal bases were covered by the *front* of the hypostome. This can be contrasted with a recent expression of opinion by Störmer

(1951, pp. 112, 117) who gives the hypostome vertical lateral walls, attaches the antennae to the side walls, and places the mouth high in the posterior wall. Contrast also Handlirsch (1926, p. 211) where the antennae are attached to the ventral surface to right and left at the mid-length of the hypostome, to the rear of which the mouth opens through the same surface, and behind this four pairs of appendages are crowded into less than the length of two segments.

As regards the number of observed cephalic biramous appendages, which are claimed to be four, this seems to depend very largely on specimen 217 of *Triarthrus eatoni* (Hall) (= *T. becki* Green) figured by Beecher (1894) and by Raymond (1920, pl. 1, fig. 3), which is supported by Specimen 211, so that it may be correct. But in neither case can we be sure of it. Walcott also came to the same conclusion as regards *Calymene* and later regarding *Neolenus serratus;* though no one who carefully studies the evidence could find it conclusive as regards either. It is difficult to avoid the suspicion that if the workers had not believed in near relationship of trilobites to Crustacea some different number than four might have been found: the writer suspects there are only three. But, since the most primitive trilobites undoubtedly display six normal segments equally developed morphologically behind the hypostome and the rostrum, these must primitively have borne six pairs of normal appendages. This is supported by the fact that the Arachnida which are derivable directly from the trilobite, have six pairs of appendages on the head, none of which are comparable with, or are homologised with antennae. We can therefore feel confident that *Triarthrus* and *Neolenus* which are primitive also bore six pairs, and if four are present in the fossils, the two pairs of appendages belonging to the two segments of the "anterior glabella lobe" were in these greatly reduced and modified.

Störmer also claims relationship of the Chelicerata to trilobites, though not descent from them; but he claims for the prosoma of the former the addition of two or three extra post-oral somites (1944, pp. 133 and 135).

Regarding the homology of the biramous limbs of trilobites, the earlier writers regarded them as comparable with the post-cephalic limbs of Crustacea and as consisting of endopodite and exopodite. Later, doubt has been expressed as to the homology of the gill branch. Störmer, recently, has specially studied the biramous limbs of the Mid-Ordovician trilobite *Ceraurus pleurexanthemus;* and has made section-series (by grinding) from Walcott's original collection from the Trenton limestone. He claims: that his series demonstrates the presence of a pre-coxal element; that the gill branch generally called exopodite, is attached to this basal element, and that it therefore represents a pre-epipodite, not an exopodite. According to him there is therefore no homology between the exopodite of the crustacean and the supposed exopodite of the trilobite (1939). The existence of an apparent discrepancy had long been known (Borradaile 1917), for the endopodite and exopodite of the crustacean are borne by the second joint of the two-jointed protopodite, whereas the two branches of the trilobite's appendage according to Walcott and to Beecher were borne by the single basal joint identified as coxopodite. But reduction to disappearance of the basipodite would eliminate the discrepancy, for it is not possible to homologise the appendages, joint for joint. If Störmer is correct the discrepancy is more serious. The writer is not qualified to judge, and must await the result of further research. But the trilobite as already stated was in the writer's view very much more primitive than the contemporary crustacean, which in turn was much more primitive than most Crustacea of today: also, biramous limbs are older than trilobites or Crustacea. It is unfortunate that *Ceraurus* bears the least primitive of the known biramous limbs of trilobites, but that probably would not affect the result.

Beecher believed that behind the hypostome there was a metastome, and Raymond (1920) and Störmer (1951) added this feature to their restorations of *Neolenus*. But the photographs do not lend support; and in such primitive forms the existence of such a specialisation there is improbable.

12. DISTRIBUTION AND ATTACHMENT OF THE POST-ANTENNAL CEPHALIC APPENDAGES

As to the distribution of the biramous limbs on the head, views have hitherto been controlled by what is seen in the fossils; and

as only *Triarthrus eatoni* has clearly exhibited the limbs under the head, this has determined nearly all restorations. Beecher believed that the limbs were entirely excluded from under the hypostome. In the fossils (Raymond, 1920, pl. 1, figs. 3 and 4; pl. 2, fig. 5) this appears to be the case. As seen from the ventral side each limb also appears to overlap the adjoining limb in front of it. This is peculiar, because behind, as suggested by pl. 5, figure 3, they overlap towards the rear, and this is represented in Beecher's and Raymond's restorations. They must have suffered a change of disposition.

Due to these few fossils, the biramous limbs in restorations of trilobites are entirely excluded from beneath the hypostome. And though the segments of the cephalic rachis in *Triarthrus* and *Neolenus* are just as long, as are those of the succeeding segments of the thorax, the limbs are unnaturally crowded together. (See the restoration by Beecher, Raymond and Walcott of *Triarthrus* and *Neolenus*.) In Walcott's restoration of *Triarthrus* (1918, p. 32), the distance between the axial lines of the first and fourth limbs is less than his representation of the length of several single segments of the thorax. In all the restorations, the foremost pair is opposite the metastoma, the existence of which is by no means convincing. Again in his restoration of *Neolenus* (l.c., pl. 31), the median ends of the "coxopodites" are so spaced that their axes are within about the length of a segment—three pairs of limbs to the length of a segment—notwithstanding that the cephalic segments are as long as the thoracic. The same applied to restorations of *Calymene* (l.c., pl. 33). Raymond however (1920, p. 55), by reducing the size and increasing the transverse separation of the anterior two pairs, puts these at the side of the hypostome. Only in his restorations of *Ceraurus* and of *Isotelus* does he represent them at all as under the hypostome: in the former the marginal brim of the hypostome covers the median end of the foremost pair, and in the latter the coxopodites of the anterior two pairs are under the posterior wings of the same.

There are, the writer believes, two basic errors behind all these restorations. Firstly, it seems probable that the crowding of the appendages behind the hypostome, which two specimens of *Triarthrus* suggest, is to be referred to the mode of entombment. The specimens lay on their backs, and a rain of sediment tended to flatten them out. The hypostome, however, prevented sediment from entering the space beneath it, and after the muscles had decayed, the load of sediment above the hypostome caused it to yield, and it pressed out much material from beneath it and so crowded the appendages together. The view-point of the second error is illustrated by Raymond's longitudinal section of the trilobite (l.c., p. 18) which is fully endorsed by Walcott (1921, p. 126). The mouth is supposed to be at the posterior tip of the hypostome, between it and the supposed metastome, which Beecher claimed for *Triarthrus;* and which Raymond added to *Neolenus*. The ventral membrane too descends to meet the tip of the hypostome at the mouth. This has perhaps been the view of paleontologists for nearly a century. A slight improvement was made by Richter (1925, p. 169) who represents the mouth as being just in front of the posterior doublure of the hypostome in *Phacops* and the supra-oesophageal ganglion as housed inside the bowl of this part, its primary position for the arthropod, but his median ventral nerve cord is opposed above. Störmer's section of *Ceraurus* is on the same lines: in his latest (1951, p. 117) the mouth is dorsad of the rear of the hypostome.

In primitive trilobites such as *Zacanthoides*, *Albertella*, *Neolenus*, the hypostome is long, ovate, and convex. Its anterior boundary is the curved, sutured junction with the narrow doublure (or rostrum), but the rest of its periphery is furnished with a doublure and was free, i.e., *having a dorsal boundary of its own* independent, except in front, of the ventral surface of the cephalon bearing the mouth and limbs. At the sides, at about mid-length, is the sharper curvature marking the points of emergence of the antennae. That the hypostome was free except round the front is not only suggested by its doublure, but also by comparison with that of the crustacean most primitive in this respect, *Apus*, a longitudinal section of which helps us to understand what would obtain in the primitive trilobite. That the hypostome was free is suggested further by the facts that (?) four pairs of normal appendages have been found under the head in *Triarthrus*, and that segmentation for six of such pairs is seen in the rachis of primitive trilobites. In *Apus* the cuticle is so thin that

though the boundary of the labrum in front is not a hinge, muscles change its shape and so change the distance between it and the appendages that are covered by it. Substitute the primitive trilobite for *Apus*, the hypostome for the labrum and the statement is true for the trilobite. The mouth in *Apus* is very far from the free end of the labrum, being according to Lindström about opposite the anterior third of its length. But after the proto-crustacean branched off in Precambrian time the normal appendages of the Crustacea have been reduced in number apparently from six to four, if the crustacean antennules are really homologous with the trilobite antennae: all have lost their ambulatory function; and as mouth parts, except for the mandibles, they have been greatly reduced in size. We can well believe therefore that the mouth has migrated rearward from a still more anterior position. The business-ends of the mandibles work entirely under cover of the labrum.

Walcott figures a beautiful photograph of *Apus lucasana* showing the strong mandibles under the labrum followed by the two small pairs of maxillae. On the same plate, beneath it, is a photograph of the hypostome of *Neolenus serratus* with (in dark shading) the arches on either side, behind which the antennae emerged (1918, p. 208 and pl. 36, figs. 4 and 3). See also Lindström, who represents the position of the mouth in *Apus* in longitudinal section and the narrow doublure of its labrum (1900, pl. 6, 46–48). In connection with our present subject the last named work deserves close study, for it illustrates the doublure of the hypostomes, though mostly in later and more specialised trilobites. Many of the hypostomes show beautifully the curved sockets for emergence of the antennae, and in several cases apodemes at the right and left angles in front for the muscles controlling its convexity and so also its position in regard to the appendages more or less covered by it.

The musculature of these appendages has already been briefly discussed. There can be little doubt as to the general position of the latter under the cephalon in the primitive trilobite. This was determined by the clear segmentation of the glabella and occipital ring, modified as this was in many cases in relation to the muscles.

Regarding the attachment and musculature of the biramous appendages, Beecher, Walcott and Raymond have furnished the restorations of the ventral surface with appendages; and Walcott, Raymond and Störmer have discussed their emplacement and musculature, especially the last named. Walcott represents them as attached to the ventral membrane, and in *Ceraurus* each in relation to an apodeme (1918, pl. 34). Raymond imports the apodemes into *Neolenus*, and figures and describes the appendages as articulated to the apodemes, which he calls "appendivers" and represents as extending through the ventral membrane (1920, pp. 24, 30, 51–52 and 60, figs. 2, 7 and 19). Störmer adopts the term appendifer and claims that the appendage was attached to it by muscles (1939, pp. 166, 176, pl. 11, fig. d). The segmental appendage, he claims, belongs to the apodeme at the front of its segment. But appendages are segmental, the apodemes are intersegmental, though with evolution they may depart somewhat from this position. In Polychaeta the muscles moving the parapodia are attached mainly at the boundary of the segment fore and aft; and in primitive Crustacea these muscles extend across the segment from front to rear. In Trilobita we can be sure that the muscles were attached, not to one apodeme but to two. It may further be mentioned that apodemes are secondary, developed more especially in later trilobites: in primitive forms we do not see them: here the muscles would be attached to the intersegmental infolds. It is probable too that the appendage muscles were also attached to the infolds forming the dorsal furrows as suggested by Walcott (1921, p. 384). Attachment to a single small apodeme as claimed by Raymond and by Störmer would be an ineffective musculature. We can conclude from this discussion that the positions of the appendages under the cephalon in primitive forms was determined by the clear segmentation of the rachis, modified as this was in many cases in relation to their specialisation and musculature.

13. DEVELOPMENT OF THE ANTERIOR END OF THE GUT IN TRILOBITES AND OTHER ARTHROPODS

Only the most primitive trilobites (largely Lower and Middle Cambrian) exhibit fully the primitive segmentation in the head and would doubtless possess six normal pairs of appendages besides the antennae. In most

others the glabella narrows to the front and there shortens; and loses, first there, the anterior, one, two or even three glabellar furrows. This can be attributed with confidence to reduction or loss of the anterior normal appendages under cover of the hypostome, in a space which became a new effective anterior extension of the gut.

In the evolution of the polychaet both appendages and their neuromeres were carried up the alimentary canal (Raw, 1949); and in the trilobites, the same change in effect took place, e.g. in the Dicellocephalidae (Upper Cambrian and basal Ordovician) only the two posterior head appendages are behind the hypostome; and owing to the great width of the cephalic doublure, there was only room for these and the antennae to reach the exterior. The remainder were in effect shut up in the space above the hypostome, which had become an extension of the alimentary tract. Confined in this space we can well imagine that they had suffered reduction and modification (see Walcott, 1914; Ulrich & Resser, 1930).

In agreement with this conclusion we may note that in most *Dicellocephalus* species only the occipital furrow and the last glabella furrow are appreciably developed. The furrow next in front is reduced to two extremely faint transverse impressions, and the remaining two cannot be seen at all. As a further indication of reduction of the anterior appendages it is easily seen that the remaining part of the glabella corresponding to the three anterior segments measures only half the length and much less than half the space occupied by the posterior three.

But this is so characteristic of trilobites in general that most workers have claimed only five segments in the axial lobe of the head and Bernard supposed that some had less than that. So general is it that in the systematic paleontology of trilobites only a frontal lobe, three glabella lobes, and the occipital are recognised; and the frontal lobe, though it represents two segments, is very often shorter than the next which represents one. Further, in the great majority of trilobites the axial lobe narrows greatly to the front.

Both the reduced number and the extreme obliquity of the glabella furrows often testify to modification of the appendages as a result of the presence of the hypostome.

When we consider the Asaphidae, a family related to the Dicellocephalidae, but more specialised, study of its genera is facilitated by the stronger exoskeleton, which makes possible good exposures of the fossils. At its first appearance in the Upper Cambrian just above the range of *Olenus* s.s. the family characters are already fully developed: it disappears in the Ordovician. With the strengthening of the shell and perfect enrolment there is a tendency toward development of a smooth surface, and the segmentation of the glabella is seldom visible, though often clearer in moulds of the inner surface. It is in this family, thanks perhaps to wide doublures, that Pander's organs are visible (see Sec. 8): a smooth node too, often seen near the rear of the glabella, is probably a median eye.

At the outset in the Upper Cambrian we have relatively primitive hypostomes, but already of two contrasted types—that of *Promegalaspides* leading towards *Asaphus*, *Isotelus* and *Ptychopyge* etc.; and that of *Niobella* leading to *Niobe* (Westergård, 1939). This study is possible largely by reason of the careful drawings by H. Bundsen and G. Liljevall illustrating the papers by Brögger 1886 and Lindström, 1901.

All the most primitive hypostomes have a semiovoid body, broad end in front, which we can call the "ovoid." This is bordered by a furrow, very narrow in front, followed by a rim. In front across the hypostomal suture it joins the doublure. At the sides in this family the hypostome is furnished with wide posterior and anterior wings. The posterior wings extend horizontally outward and rearward, and between them, behind the ovoid, is a deep median embayment. These posterior wings are clearly quite free from the ventral surface of the head above them, for, throughout, they have a doublure on the inner or dorsal surface. In several forms they extend rearward almost to the limit of the headshield (see e.g. *Asaphus nobilis* in Barrande 1852, pls. 31–33): it is quite clear that the posterior biramous appendages were attached under their cover, and that their basal joint operated there. These wings diminish in width to the front, and die away against the side of the "ovoid."

The anterior wings lie dorsad of the posterior wings by which in ventral aspect they are overlapped. They bend dorsally rather steeply on each side; but in front they are continuous with one another by the narrow marginal furrow. The anterior wings have no doublure: in *Asaphus* they have an anterior curved boundary at the hypostomal suture, across which they join the doublure of the cephalon; but laterally they presumably joined the uncalcified ventral cuticle and there is an angle between these two boundaries. In *Ptychopyge angustifrons*, however, and in other forms where the cephalic doublure is greatly widened (e.g. *Niobe*) the whole of the external boundary of the anterior wings, a continuous curve of half a circle or more, directly joins the doublure over the hypostomal suture. As the two sets of wings have different levels and different directions very frequently one set only is seen in fossils.

At the sides, where the posterior wings overlap the anterior, in all genera the cuticle of the anterior wings passes over into the cuticle of the doublure of the posterior wings, forming the beautifully rounded and curved channel through which, as the writer claims, the antennae emerged. In *Ptychopyge angustifrons*, where the doublure is so wide, it is clear that the antennae could not emerge anywhere else; and this indicates what was general. It is clear too that the space in front of this emergence and covered by the anterior part of the hypostome-labrum was enclosed, and with its appendages had been added to the alimentary canal: the anterior wings in *Asaphus*, also, by their dorsal bend were enclosing the same space. It was nature's mode of invagination of that part of the stomodeum. Behind the antennae there was room for two (or three) pairs of biramous cephalic appendages to serve the mouth and for locomotion, and the writer fully agrees with Raymond that their basal joints worked under the wings of the hypostome. Raymond in his restoration of *Isotelus* gives four pairs of cephalic biramous limbs, two under the hypostome wings and two behind (1920, p. 38, pl. 10, fig. 2); but this is pure hypothesis based on *Triarthrus*, for both he and Walcott reproduced photographs of the specimen on which the restoration is claimed to be based (Walcott, 1918, pl. 24), which show only nine pairs of limbs with large coxopodites followed by less distinct and smaller limbs which must belong to the pygidium (U. S. Nat. Mus. no. 33458). Of the nine pairs of large limbs eight must belong to the thorax leaving only one pair belonging to the head in the specimen, which however is incomplete in front. In the asaphid there is not room for more than one pair of appendages, that belonging to the occipital segment to be free of the hypostome; and hence it is probable that the specimen shows only this pair. The others working under the hypostome would probably all be reduced to some extent. We must await a still more fortunate find.

In front of the normal appendages of the asaphid cephalon there lies a great problem, much of which can never be solved by fossil evidence. To this many solutions have been offered by others. Much of the writer's view has already been given and will be summarised here.

In the polychaet the mouth was on the peristome, which in the arthropod, on our theory, is represented, as to its tergum, by the rostrum. The primitive position of this on Bernard's theory may have been about vertical; but, situated between the strong convex hypostome and the similar dorsal rachis it has suffered great change in the trilobite. In several families, however, it remained a separate plate, bounded all round by sutures—rostral, hypostomal and the connecting sutures (e.g. Centropleuridae, Illaenidae, Scuttellidae, Ptychoparidae, Calymenidae, Eucrinuridae, Cheiruridae and others). In Olenellidae and most Paradoxidae it is ankylosed to the hypostome, and in Phacopidae it is coalesced at its ends with the free cheeks. The loss of sutures can be attributed to the retention only of those necessary for ecdysis. It may be greatly extended, as in the Olenellidae; or it may be eliminated, as in Olenidae, Dicellocephalidae and Asaphidae. The antennae have above been referred to the rostral segment, but the form of the rostrum does not suggest any connection with appendages: no muscle impressions pit its surface. Its main function in the cephalon would seem to be simply to form part of the strong edge of the shield and to take a share in its change of shape. For the terrace lines which in primi-

tive trilobites characterise the whole of it, as well as the rest of the doublure can best be referred to muscle attachment for changing the shape of the shield. Hence if the antennae are to be ascribed to the rostral segment, a secondary musculation would appear to have developed before Cambrian time; and it may well be that the "antennal pits" are related to such a musculature.

Above the hypostome, here bounded by its own uncalcified cuticle inherited from the pro-arthropod, were the appendages of the glabella segments, attached dorsally to the ventral cuticle of the head. Originally in the prot-arthropod they were arranged with segmental regularity and some primitive trilobites have such regular segmentation, that their appendages might still be regularly attached, notwithstanding the arching of the body front into a semicircle. But in the evolution of the trilobite class as in other arthropod classes one after another these appendages would become more and more reduced and adapted to new functions. Already in the Precambrian the trilobite ancestor of the arachnid s.l. had reduced its anterior pair. Three joints only exist in the Xiphosura, scorpion and eurypterid; but behind this, little reduction took place apart from suppression of the gill branch. In the trilobite, however, much greater and more varied evolution of the cephalic limbs occurred. This was associated, and probably connected with the retention of the antennae: the great importance of these would lead to their development, which in turn one can well believe would lead to marked reduction of the biramous appendages above them; while, owing to their continued partial enclosure, these ceased to be ambulatory and respiratory, and took on alimentary functions. A pair of them would probably come to constitute the appendages at the secondary mouth opening, and in front of this along the new extension of the gut the reduced and modified appendages occurred in an order *the reverse of their morphological order* —No. 3 being followed down the gut by No. 2 and this by No. 1. It is the view of the writer that, what had happened three times over in the evolution of the polychaet, in effect happened yet again in the evolution of the arthropod (Raw 1949).

TABLE 1.—SEGMENTAL POSITION OF REAR OF HYPOSTOME AND OF ANTENNAL EMERGENCE

Trilobite species grouped in families	"Segmental" opposition of:	
	Rear of Hypostome	Antennal Notches
Dalmanites hausmanni Brongn.	5	2
D. socialis Barr.	5	2–3
Phacops fecundus Barr.	5–6	2–3
Cheirurus gibbus Beyr.	5–6	2
Amphion fischeri	5–6	3–4
Scutellus palifer Beyr.	5–6	3
S. companifer Beyr.	6	3–4
Paradoxides bohemicus Boeck.	4–5	3
Remopleurides radians Barr.	4–5	2–3
Proetus bohemicus Cord.	5	3
Conocoryphe sulzeri Schlot.	5–6	3
Calymene blumenbachii Brongn.	5–6	3–4
Nileus armadillo Dalm.	6	?2
Asaphus expansus Linn.	5–6	?2
Asaphus nobilis Barr.	5–6	?2
Lichas incola Barr.	5–6	?
Harpides grimmi Barr.	5–6	?
	Two figures imply the junction of segments, e.g. 5–6 is the neck furrow.	
	In front of these positions the normal appendages were entirely or partly under the hypostome.	In front of these the appendages became enclosed within an extension of the gut.

This is not a new principle: Janet (1899, 1909) had the idea long ago. He claimed the existence of nine segments in the head of the insect. But his was a speculation based on the extent of the stomodeum as well as on the known cephalic appendages. He knew nothing of the close comparison that can be instituted between the polynoid and the trilobite (given above): also nothing of the evidence for the number of segments represented by the head of the polychaet (Raw 1949, pp. 1–19). Had he known these, he might have claimed that ten segments were represented, seven from the prot-arthropod and three from the polychaet, and yet some behind the polychaet. But thanks to the abundant evidence furnished by the trilobites the principle will be found to bring all true arthropods into line and cause them to be considered as monophyletic.

It is instructive to compare closely the ventral side of the cephalon with the opposing dorsal side to see to what segments the ventral structures are opposed. The accompanying table is compiled from a comparison which Barrande made possible by his carefully drawn figures. It shows the position of the rear of the hypostome and of the notches on its sides through which the antennae appear to emerge relative to the segments, 1–6, of the opposing cephalic rachis.

In *Phillipsinella parabola*, which Whittington with good reason erects into a new family, the rear edge of the hypostome according to his restoration extends even beyond the rear edge of the occipital segment: with this is associated great axial length of the rostrum (Whittington 1950, fig. 8 and pl. 75.)

14. INTERPRETATIONS OF THE TRILOBITE CEPHALON FROM 1849 TO 1951; FIGURE 5

The interpretation of the trilobite cephalon developed in previous sections, is in such marked contrast with all others that have been proposed, that it is well to halt, and relate it to some of the others that have appeared within a century. Its unique character results from: I, its basis in the most primitive forms; II, the recognition of its relationship to the polychaet, and its composition out of the eight anterior elements of the same, the foremost of which is besides very complex; III, the recognition of the loss of external cephalic appendages, and their incorporation in an anterior extension of the gut; and IV, the allocation of the trilobite antennae.

Practically all previous writers compare the trilobite most closely with the crustacean, though Holmgren was impressed with its arachnid affinities. But whereas the earliest writers, M'Coy 1849, Walcott, and Beecher 1897, and following them, Raymond 1913, and Störmer 1942, 1944, have equated the trilobite cephalon to the crustacean head bearing the first five pairs of appendages, several later writers, following Jaekel 1901, have seen in it a greater number of segments. Jaekel himself, Warburg 1925, Henricksen 1926 and Richter 1932 included also a first maxillipedal; and Holmgren 1916, a second maxillipedal also, equated with the fourth walking leg segment of the arachnid.

All those writers have recognised, in front of the appendage-bearing segments, a single ocular segment, of which the free cheeks bearing the eyes were considered its pleura: but, for its tergite, whereas M'Coy, Warburg, Richter and Störmer named the preglabellar field, Beecher, Raymond, Jaekel and Henricksen named the rostrum: M'Coy, however, had named this as its sternite!

The hypostome is presumably homologised with the crustacean labrum but Richter regarded it as the sternite of the antennary segment!

Only the writer homologises the trilobite cephalon with: I, the anterior part of the polynoid polychaet as far as the fourth elytriferous segment; II, with the crustacean head, and at the same time with the chelicerate prosoma; and III, these two with one another.

Of these writers, only Holmgren and the author attribute the trilobite antennae to so forward a segment. Further, it is claimed above that instead of there being a single ocular segment; all the normal segments primitively inherited eyes, and a pair also was inherited from the peristomium, besides pairs from two segments incorporated in the prostomium of the polychaet. The hypostomal eyes are inferred to have migrated from the rostrum which represents the peristome; and each compound eye is claimed to have replaced six simple segmental eyes.

A comparison of these different interpretations is given in the accompanying Tabular Survey; in which A is the symbol for the Ancient, i.e. annelid head, O signifies the primitive Oral position, and I–VI indicate the following six normal segments of the annelid and arthropod. And further to bring out the contrast of views as to the distribution of the segments over the cephalon the application of the more detailed of these interpretations to this tagma in the primitive mesoparial trilobite *Albertella bosworthi* Walcott is indicated in figure 5.

15. A SEMI-OVOID BODY-FORM AS CHARACTERISTIC OF PRIMITIVE TRILOBITES
Figure 6A–F

Very early in his studies (1923) the writer concluded that a semi-ovoid body-form was characteristic of primitive trilobites; but he has avoided any attempt to prove it, and he has not seen any appreciation of it by others. A presentation of the subject was projected for another paper; but as the present one would in that case be incomplete, some discussion of it can be given here.

While claiming the heptacicephalic, many-segmented and annelid-like form as that of the ancestor, he has hitherto derived from it only the semicircular heads of proparial, mesoparial and metaparial trilobites; but he has also stressed the convexity of forms preserved in limestone or sandstone in contrast with the flattened character of those preserved in shale or slate. This is illustrated by the lateral elevation of *Callavia callavei* from the Comley calcareous sandstone of Shropshire (fig. 6E).

As mentioned at the outset, trilobites had already reached their greatest variety in the Cambrian, and probably before; and hence, in view of the extreme rarity of Precambrian fossils, we may never know earlier forms. But in the Lower Cambrian the Olenellidae range through the series and are abundant; and in the Middle Cambrian the Paradoxidae function in the same way. In both of these families falcate pleura are characteristic; and only seldom are these replaced by other forms of pleura, e.g. in *Holmia kjerulfi* and *Paradoxides bohemicus*. When they are, it is a replacement by the form characteristic of early stages of development: it is a carrying forward of the larval character into the adult; and is probably at the same time a reversion.

The significance of this falcate form of the pleura has apparently never been discussed; and so, perhaps, has not been realised by others. Little attempt has been made to represent the animals as alive. Beecher (1894) writing of *Triarthrus eatoni* (Hall) (="*T. becki* Green") states:

> It seems most probable that *Triarthrus* could both swim freely and crawl along the bottom; and that on dying they coiled themselves up like the recent isopods. Then upon unrolling they would necessarily lie upon their backs. Even if they did not coil up, any swimming animal having a boat-shaped form would settle downward through the water with the concave side up.

It may be added that this species probably

FIG. 5—Various authors' interpretations of the trilobite cephalon applied to the primitive *Albertella bosworthi* Walcott.

As all except the author recognise an ocular-segment, whose pleura are the free cheeks; and as all compare the segmentation with the crustacean,

O = ocular segment
A1 = antennular
A2 = antennary
M1 = mandibular
M2 = maxillular
M3 = maxillary
M4 = 1st maxillipedal
M5 = 2nd maxillipedal

Where data are sufficient, alternate segments are dotted, the mandibular segment being white; but for further contrast this is black at the sides of the rachis, where its position departs from that in the crustacean head X_1 and X_2 segments unrepresented by external appendages in the crustacean.

Further,

T = segment of the trilobite antennae.

Thus,

A_1T = antennular segment carrying T.
A_2T = antennary segment carrying T.
OA_1T = ocular segment coalesced with the antennular and carrying T.

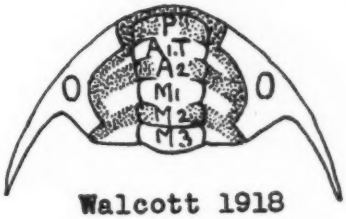
McCoy 1849

Beecher 1897

Jaekel 1901

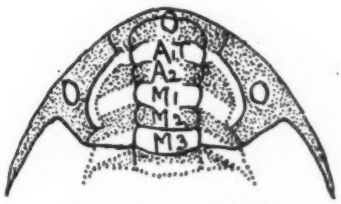
Raymond 1917
1920

Holmgren 1916

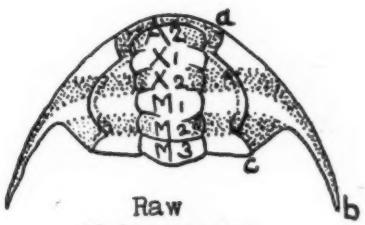


Walcott 1918

Warburg 1925
Henricksen 1926
Richter 1932



Stormer 1942
1944



Raw
this paper

TABLE II.—SURVEY OF THE INTERPRETATIONS OF THE TRILOBITE CEPHALON FROM 1849–1951

	SYMBOL AND PART	M'COY 1849	BEECHER 1897 RAYMOND 1913, 1920	JAECKEL 1901
A	HYPOSTOME	Hypostome	Hypostome	Hypostome
O	ROSTRUM	**Ocular:** its tergite—the preglabellar field; its sternum—the rostrum	**Ocular:** its tergite—the rostrum; its pleura—the free cheeks	**Ocular:** its tergite—the rostrum; its pleura—the free cheeks
I	GLABELLA 1st Dorsal Segment, with pre-glabellar field			**Antennular** no appendages
II	2nd DORSAL SEG.	**Antennular:** **Trilobite antennae**	**Antennular:** **Trilobite antennae**	Antennary: **Trilobite antennae**
III	3rd DORSAL SEG.	Antennary	Antennary	**Mandibular**
IV	4th DORSAL SEG.	**Mandibular**	**Mandibular**	Maxillular
V	5th DORSAL SEG.	Maxillular	Maxillular	Maxillary
VI	OCCIPITAL 6th DORSAL SEG.	Maxillary	Maxillary	1st Maxillipedal

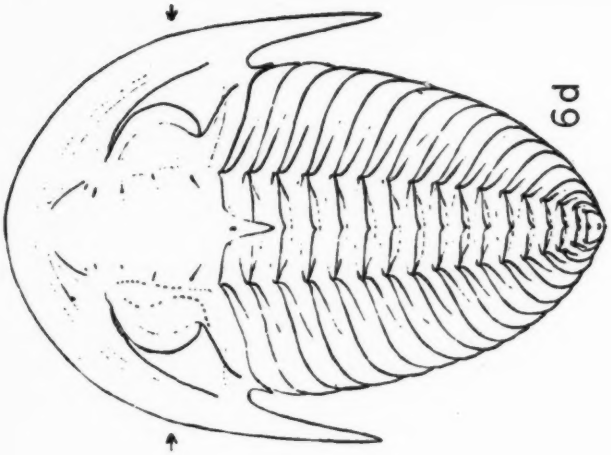
Notes: Hypostome and Occipital segment—top and bottom rows. Unrecognized segments—blank. **"Ocular** segment," **Trilobite antennae** and homologues of Crustacean **Antennules** and **Mandibles** in **boldface type.**

	HOLMGREN 1916	WALCOTT 1918	WARBURG 1925 HENRICKSEN 1926
A	Hypostome	Hypostome	Hypostome
O	**Ocular** coalesced with **antennular: antennae**	**Ocular:** its pleura the free cheeks	**Ocular:** its tergite—the preglabellar brim (Warburg), this+rostrum (Henricksen); its pleura—the free cheeks
I	Cheliceral or Antennary: No appendages known	Palpebral	**Antennular** **Trilobite "antennae"**
II	Pedipalpal or **Mandibular:** No appendage known	**Antennular** **Trilobite** **Antennae**	Antennary: No appendages
III	1st Walking leg (of Arachnid) or Maxillular	Antennary	**Mandibular**
IV	2nd Walking leg (of Arachnid) or Maxillary	**Mandibular**	Maxillular
V	3rd Walking leg (of Arachnid) or 1st Maxillipedal	Maxillular	Maxillary
VI	4th Walking leg (of Arachnid) or 2nd Maxillipedal	Maxillary	1st Maxillipedal

TABLE II.—(*continued*)

	RICHTER 1932	STÖRMER 1941, 1944	
A	Hypostome (Sternum of Seg. II)	PREORAL	Hypostome?
O	**Ocular:** its tergite—the preglabellar brim; its pleura—the free cheeks	Preantennal segment complex	Doublure with Rostrum Preglabellar field, *eyes*, extra-ocular cheeks, genal spines, and anterior part of glabella.
I	**Antennular: Trilobite antennae**		
II	Antennary: its pleurae—the palpebral lobes; its sternum—the hypostome. No appendages.	**Antennular,** Palpebral segment: **Trilobite antennae**	
III	**Mandibular**	POSTORAL. 1st Leg segment innervated by Tritocerebrum	
IV	Maxillular	2nd Leg segment = **Mandibular**	
V	Millillary	3rd Leg segment	
VI	1st Maxillipedal	4th Leg segment	

	RAW (this paper)			Corresponding "somites" in POLYNOID POLYCHAET
A	Hypostome: its 2 pairs of *eyes* had migrated to dorsum; 1 pair of *eyes* (maculae) from rostrum			Prostomium Complex
O	Rostral: its tergite the rostrum; its *eyes* had migrated to hypostome; **antennular: Trilobite antennae,** innnervated by deutocerebrum			Peristome
I	**Macrosomite** (with **pro-cranidial spines**) = Cheliceral. Appendages unknown; innervated by tritocerebrum			1st Normal segment; Elytriferous
II	= Pedipalpal: appendages unknown			2nd Normal segment
III	**Macrosomite.** Appendages?	Pleural spines coalesced into **parial.**	**Dorsal ocular** segments. All eyes, simple and compound, innervated secondarily by brain	3rd Normal segment; Elytriferous
IV	**Macrosomite. Mandibular** Biramous appendages			4th Normal segment; Elytriferous
V	Biramous appendages			5th Normal segment
VI	**Macrosomite,** with **metacranidial spines.** Biramous appendages			6th Normal segment; Elytriferous



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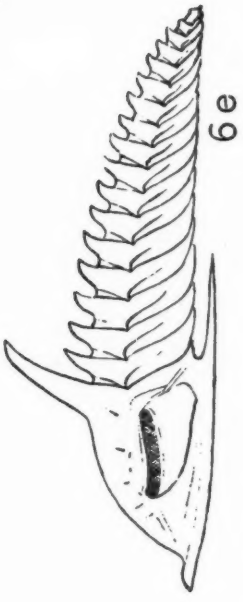

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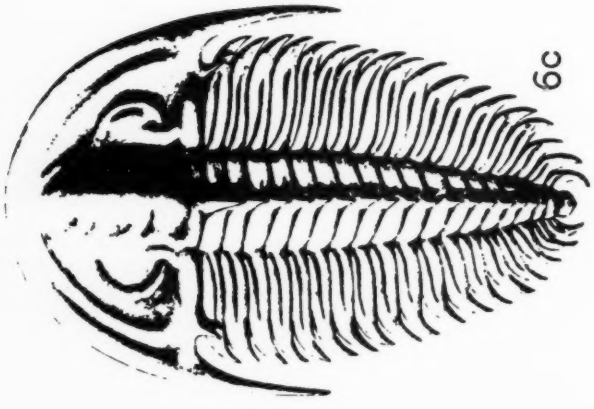

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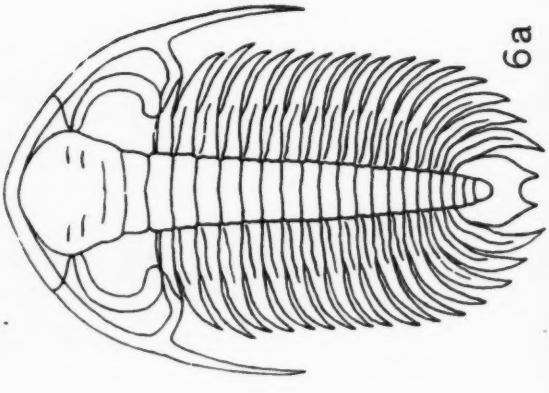

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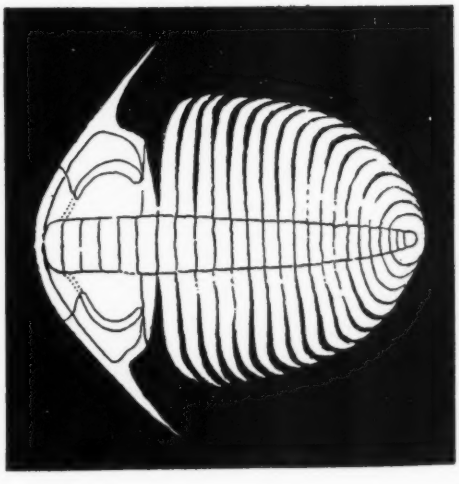

lived as part of a plankton among floating seaweed; and that the sloughed skins and dead bodies falling through the water would settle on their backs. In this position they would decay and get loaded with sediment, which would tend to flatten them out: in this position, too, the tests were free to do so.

The head and pygidium are connected with the thorax, and the thoracic segments with one another, by soft cuticle, most strongly on the dorsum. These connections extend between the pleural spines of opposite sides, i.e. between the positions dorsal of the inner edge of the doublures of the pleura (see Westergård, 1936, pl. 2, figs. 4, 10). In primitive forms the pleura are chiefly spine; and, even in broad forms like *Olenellus* and *Paradoxides* with very small pygidium, the posterior pleura have their doublures extending up to the rachis: i.e. they are all spine. On the principle, that this is where the most primitive segments occur, it follows that in the ancestral prot-arthropod the pleura were free, as in the foliate lobes of the annelid parapodia; and that they had doublures of strengthened chitin. Normal trilobite pleura thus consist of two distinct parts: the outer, bounded below by doublure, which when pointed, is called the pleural spine; and the inner, which may be rectangular or curved, and was bounded below by soft cuticle. The outer part was inherited from the pro-arthropod through the prot- and deut-arthropod; the inner which especially characterises the trilobite, is a secondary development, evolved in this class; and was one of the means whereby the semi-ovoid body-form was developed, the other being the widening and shaping of the pleural spines themselves. This form was precedent to all enrolment, later evolved in the majority of families.

Besides the Olenellidae and Paradoxidae other families in considerable number have falcate pleura such as Redlichiidae, Olenopsidae, Dicellocephalidae, Zacanthoidae, Remopleuridae, Scutellidae and Lichidae. Besides these, again, there are many families, in which some members, usually early members, have pleura of the same form; whereas later forms have rounded ends better fitted for enrolment. Such are Bathyuriscidae, Asaphidae, Anomocaridae, Ptychoparidae, Conocoryphidae, Proetidae, Otarionidae, Illaenidae, Styginidae, Ellipsocephalidae, Phacopidae and Cheiruridae; besides several Pacific region families.

It will be agreed that *Paradoxides* is a primitive genus, as indicated by its thin test, its simple and complete segmentation of the head rachis, its preservation of metacranidial spines for early stages, and retention of the parial for the adult, its simple and numerous thoracic segments and its small and simply structured pygidium with only one or two segments defined (see Westergård, 1936 for early *Paradoxides*). Throughout the genus the pleura are almost always falcate and end in flat thin pleural spines. The anterior and posterior boundaries of these are practically identical in outline, except that, owing to the rearward curvature, the anterior extends further to the rear. Hence by a little bending, the pleural spines would all fit together, edge to edge, without interfering at all with forward progression; and the writer claims this as the function of the falcate form of pleuron. In life the habitual body-form was a semi-ovoid: the head was a modified quarter-sphere; the pygidium was a smaller section of a spheroid; and the thorax was so arched, transversely and longitudinally, that the pleura all fitted together edge to edge forming lateral and posterior walls. The anterior pleura extend transversely before curving rearward into the pleural spines; but the two strips made by their

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FIG. 6*A–F*—Typical illustrations of the semi-ovoid body-form characteristic of primitive Trilobites.

A—*Paradoxides rugulosus* Corda, as found, flattened in shale (Raw 1927, Fig. 15, p. 132).

B—Ideal "semi-ovoid" trilobite drawn on the surface of a semi-ellipsoid of white rubber, cut out and the pleural spines separated.

C—Professor Lapworth's restoration of *Callavia callavei* (Lapworth), based on specimens of *Callavia bröggeri* (Walcott) from shale (Lapworth 1891, pl. 15).

D—Author's restoration of the same based on its convexity. A transverse section along the line of the arrows is given as fig. 4*G*.

E—Restoration of the lateral aspect. (Unfortunately, in *D* and *E*, 16 segments instead of 18 are represented); (*D* & *E* from Raw 1936, p. 279, and 1937, p. 581, with thorax added.)

proximal parts taper rearward, and are replaced by pleura curving rearward more and more. This adapts the pleura to fit the narrowing rear of the ovoid; and the posterior radiation of the pleural spines is an adaptation to the same end. The primary function of all this was probably to control the flow of water past the gills, the water entering under the front of the head, which is there somewhat uparched, and escaping around the pygidium. In *Paradoxides* as well as in many Olenellidae the fact that the fit is perfect also around the pygidium, suggests that a further function of this part was to facilitate ploughing through the mud by exerting a posterior push when the arched rachis was straightened (compare with the use of the tail spine by *Limulus* in digging).

During fossilisation the part surviving decay was the stronger cuticle; and this would be the case also in sloughed skins. Then, as the tests lay on their backs, they were loaded with sediment, and flattened out. Along the thoracic rachis each articulating half-ring is joined by soft cuticle to the rear of the segment in front; so telescoping to the horizontal is easy. But there is no possibility of much movement between the successive proximal parts of the pleura, which however extend more nearly horizontally and so do not need it. On the other hand the pleural spines are free from one another, and in the flattening the lateral walls that they constitute, break up into the spreading pleural spines. The flattening involves then mainly: telescoping of the rachis; and outspreading of the pleural spines. This applies to all the forms with falcate pleura: in life they were semi-ovoids, with continuous lateral walls applied to surfaces of various kinds. It may be added here, that in this flattening through sedimentation, the rachis, more especially throughout the thorax, has been greatly deformed; the arch changing from semicircular to depressed or even greatly flattened. No allowance for this was made either by Beecher or Walcott in their restorations.

The truth of the above claim is indicated by the fact that a little bending of the pleural spines will make them form the continuous lateral walls; and that the restorations so made are in agreement with one's knowledge of the parts. The claim is illustrated by the restoration of *Callavia callavei* (Lapworth) which unfortunately was represented as having 16 instead of 18 segments. Lapworth's original restoration is also reproduced for comparison.

The disposition above deduced was that of the primitive trilobite when stationary; and that this was usual, is suggested by the eyes—semicircular, with vision all round. The arching of the pleura was probably effected by muscle contraction, the muscles being attached to the terrace lines of the doublures. The pleura may then in many cases have been held in this position by the surrounding sediment. When the animal walked or swam the pleura may, by their own elasticity, have changed to a more nearly horizontal position. Many of these forms with falcate pleura would enroll when in danger; and this enrolment would determine: 1, the evolution of larger pygidia, modified to fit the head; 2, the shortening and rounding of the pleural spines; and 3, the development of gliding facets.

When, however, trilobites with falcate pleura were entombed dorsal side up, the tendency to telescope the rachis would be at a maximum; but in Olenellidae this would be opposed by the external articulation, first noted by Kiaer (1916, p. 79) and further illustrated by Raw (1936B, p. 257, and pl. 18, figs. 6, 7, 8 and 19). Such entombment dorsal side up may well explain the peculiarity of the few known specimens of the Middle and Upper Cambrian proparian family, Burlingiidae. The family is represented by *Burlingia hectori* Walcott (Walcott, 1908, p. 15 and pl. 1) and *B. laevis* Westergård (Westergård, 1936, p. 32 and pl. 12) of the Middle Cambrian; and by the Upper Cambrian *Schmalenseeia amphionoura* Moberg, (Moberg 1903, p. 93 and Tavl. 4; Westergård, 1922, pp. 119, 192 and Tavl. 1). They are very small, ranging from 13 mm. long (*B. laevis*) to 2.8 mm. (*Schmalenseeia*): their pleura are truncated falcate, but the ends are not separated in the fossils. On the other hand there is evidence of much telescoping of the rachis and of the proximal parts of the pleura, which was facilitated in each case by their smooth or even surfaces. The family is of great interest, because: I, though both genera exhibit about the same

total number of segments, the earlier, *Burlingia*, has a pygidium exhibiting one segment only, whereas the later, *Schmalenseeia* has seven segments in it; II, on the other hand, the earlier has a cephalic rachis relatively smooth, whereas the later has very clear segmentation in it! III, it is one of the first examples of the evolution of a smooth, i.e., evenly rounded test; IV, it exhibits so clearly the mode of origin of the pygidium, which is also seen in Olenellidae and Paradoxidae, namely, by the union of a pair of pleura in the mid-line, under which, apparently, the useless segments behind aborted (Walcott, 1910, pp. 302–3, Raw, 1936 B, p. 257, note 1). This origin of the pygidium, demonstrated by the Olenellidae, is strong evidence for a longitudinal arching of the body. Walcott described his *Burlingia* as "slightly convex," while Westergård, his as "depressed." But the writer believes that both, in life, were highly convex; and that, perhaps because they were right side up, and being smooth were easily telescoped they yielded more especially in this way especially after the soft connecting cuticle decayed. It may be noted that, in *Burlingia laevis*, the free cheeks have slid over the fixed and suggest a narrow uparched form before flattening.

If the semi-ovoid body-form is the proper interpretation of the falcate pleura of the Olenellidae and Paradoxidae, what, it may be asked, is the significance of the usually different pleura of the Olenidae?

As claimed above, the pleura primitively were quite free, and were covered below by cuticle strengthened like that of the dorsal surface. But in the development of the semi-ovoid, the proximal united parts of the pleura were evolved by means of interstitial growth between the rachis and the primary pleura; and they are covered below by the delicate ventral cuticle. In the Olenidae s.l., which so characterise the Upper Cambrian, and at least as the Triarthridae continued through the Ordovician, only a limited number have falcate pleura; mostly these parts are truncated by the external boundary of their pleural spines, as in their meraspid larvae and in similar stages of Paradoxidae and Olenellidae. But the proximal parts have a much greater dimension than have the pleural spines; and hence on the writer's theory they also have descended from forms with a semi-ovoid body applied to a surface. It is therefore suggested that they have taken to a new and very active mode of life, in which larval characteristics were still useful for the adult; indeed that the adult as well as the larva was pelagic, living among floating seaweed. This would accord with their frequent occurrence in black shale, and with the development of long spines and sub-spherical eyes; and with the forward advance of the parial spines, in *Ctenopyge* and *Sphaerophthalmus*, owing to the fact that the procranidial spines had already been lost. The great convexity of these forms, when alive, is indicated by the shapes of those from little-compacted sediments, which contrast so markedly with those from shale (see Westergård, 1922, Tavl. 12, fig. 1b; Tavl. 13, figs. 9 **a, b, c;** 20a, b, c; 30a, b, c; and contrast these with the shale specimens figs. 22, 23, 31 and 32).

The number of segments which have aborted behind the effective termination of the body, however this was brought about, is probably very great. Primitive polychaets can have hundreds of segments and primitive trilobites can have great numbers. In the Olenellinae where the effective boundary is at the 15th post-cephalic, *Olenellus robsonensis* (Burling) has according to Burling (1916) more than 44 post-cephalic segments.

16. STAGES IN THE EVOLUTION OF THE ARTHROPOD AND OF THE TRILOBITE
Figures 7A–E

Two opposite views have been held as to the origin of the arthropod. They were discussed by the writer in 1927 (pp. 16–23). Matthew, Beecher and Raymond, then opposed, have been followed recently by Störmer. All have assigned to the stages of development a relatively exact phylogenetic significance. On it Beecher based his ascending scale of orders, and placed the Agnostidae and Eodiscidae with the fewest segments at the base of his system. Raymond derived the trilobite from an unsegmented "worm" comparable with the modern *Spadella*. Störmer in turn derives them from a form like the early protaspis of the Olenellidae; and, claiming that its marginal suture is primitive instead of secondary, de-

rives the Hypoparia or at least the Cryptolithidae (Trinucleidae), the Proparia and the Opisthoparia directly from it (Störmer 1941, p. 149). In this he assumes that during the ontogenies a marginal suture becomes proparial or mesoparial, notwithstanding the writer's demonstration that the marginal suture of the Olenellidae is a secondary development of the rostral and connecting sutures, due to the revolution of the procranidial spines to the genal angles; and that the dorsal facial sutures are ankylosed, though still traceable.

Those paleontologists have believed that the ontogenies of trilobites in their multiplication of the segments were recapitulating the origin of the arthropod. On the contrary it is the origin of the annelid that is there represented.

Bernard however (1892, 1894), derived the arthropod from the many-segmented polychaet and zoologists in general have supported this view. The writer supported it in 1927, and in the present paper gives his views in more detail. The accompanying figures 7A–E illustrate these theories of origin of the arthropod and of the trilobite.

If this interpretation of the trilobite, as not only the simplest of known arthropods, but as exhibiting fully the primitive segmentation of the class is accepted, it enables us to define anew the arthropod phylum by a definition of the cephalon, the only tagma which all have in common.

But the trilobite is not the original compound-eyed arthropod. This would be a very different, and much more amply segmented creature; ancestral to trilobites, chelicerates and mandibulates. For this stage the term deut-arthropod suggests itself (fig. 7E).

The compound eyes were evolved already in the heptacicephalic stage (Sec. 10). Each arose along the whole length of the free cheek at its inner limit—the ocular branch of the suture; and each was based upon a crescentic line of segmental eyes, and covered a length of four segments, as is seen in primitive trilobites (see fig. 3H).

Judging from the trilobite this eye was

FIG. 7*A–E*—Stages in evolution of the arthropod suggested by the trilobite. (Original.)

For a polychaet suggesting origin of the arthropod see *Eteone picta* de Quatrefages Fig. *1A*.

7A—Ideal polychaet with normal prostomial appendages and eyes, with notopodia like a phyllodocid (*Eteone*), segmental eyes throughout body as in a eunicid, and with merocyclism of a polynoid (subfamilies Polynoinae and Hermioninae), the merocycles being diads to segment 23 (normal segment 22) and triads behind this.

7B—The pro-arthropod suggested by primitive trilobites and their ontogenies, annelid-like in segmentation; but the terga of prostomium, peristomium and all normal segments protected by stronger cuticle and axial spines. Two pairs of eyes on the prostomium, a pair also on the peristome, and segmental eyes also on all normal segments, presumably on their pleura. Notopodia as protective pleura strengthened dorsally and ventrally, while also acting as appendages moved by muscles and bearing the pleural furrow. Merocyclism by macrosomites bearing greater axial and pleural spines.

7C—The *early* prot-arthropod.

By habitual subretroversion of prostomium and peristomium, these and the first six normal segments became the head. This originated by reduction of movement and concrescence of the adjoining pleura. It bore axial spines and four pairs of lateral spines (those of macrosomites 1, 3 and 4 and 6); also three pairs of ventral eyes and six pairs of dorsal, which last were all innervated by their segmental ganglia. With the head we have the origin of the arthropod. In ecdysis perhaps the intersegmental divisions parted as much as was necessary.

Normal segments in merocycles continued behind the head, all bearing eyes.

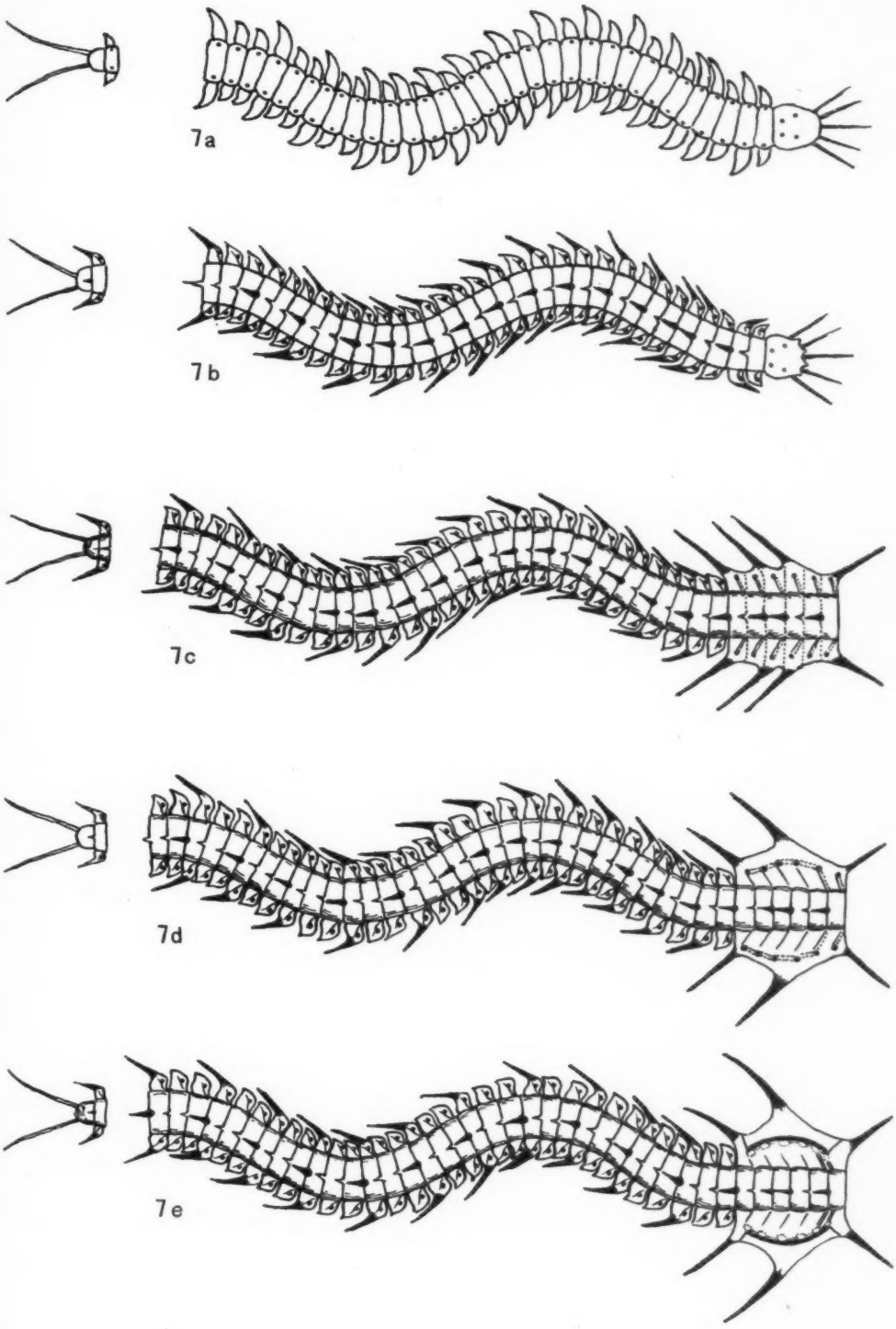
7D—The late prot-arthropod.

On the head neighbouring peripheral spines on normal segments 3 and 4 on each side have coalesced, making it heptacic; dorsal eyes have enlarged and have become innervated by way of line of eyes and nerves of an anterior pair.

This enlargement of eyes and the new continuous light-sensitive nerve along them caused the line of eyes to be a line of soft cuticle. The dorsal facial suture was thus originated, line of eyes became ocular section, whereas the anterior and posterior branches were partings between first and last pleura and the free cheek block between them. The prot-arthropod stage is recapitulated as regards the eyes in the larval development of many insects, and in the embryo of *Limulus*.

7E—The deut-arthropod.

Radiate eyes characterise trilobites, chelicerates and mandibulates; and perhaps all arthropods have these eyes in their ancestry; for the arachnids have probably lost them.


7a
7b
7c
7d
7e

evolved for the adult benthonic life; and from the insects and from *Limulus* one concludes that in the deut-arthropod it would replace the dorsal segmental eyes during the larval ontogeny.

After this stage the postcephalic body in some became triadic throughout owing to forward advance of the boundary between diads and triads, thus giving rise to the merocyclism exhibited by the higher arthropods, whereas in those that were to originate the diplopods the body may have become diadic throughout, by posterior retreat of the same.

The evolution of the various primitive types of trilobites from the heptacicephalic deut-arthropod has already been discussed by the writer (Raw 1925, 1927, 1936, 1937, and in this paper).

17. RELATIONSHIP OF TRILOBITES TO OTHER ARTHROPODS

It hardly needs mention, that our subject has an important bearing on the vexed question of the segmentation of the head in the other arthropods.

In the Arachnida it was not the normal biramous appendages that were lost, but the antennae. They are unique in retaining all the rest of the head as external appendages. The Olenellidae, with which they can be compared, retained the antennae (Dunbar 1925), and probably had seven pairs of appendages, all told, on their cephalon; and the same is true of correspondingly primitive families.

The "cephalothorax" of the Xiphosura compares closely with the head of the olenellid trilobite. The segmentation is the same: both have lost the dorsal facial sutures, which loss the writer has fully explained for the Olenellidae (1925, pp. 296–309; 1937, pp. 575–596): both depend for ecdysis on a ventral suture, which in the Olenellidae has been shown to be an extended rostral suture, stretched out in the migration of the procranidial spines, which carried the connecting sutures with them round to the posterior angles: both have a pair of "ventral" eyes on the labrum: and in both apparently the "prostomial" eyes migrated on to the dorsum. The differences between them are much less important, and include the following: 1, the olenellids apparently lost the prostomial eyes before Cambrian time; 2, the labrum in the Xiphosura has been reduced, not however before the chelicerae had been reduced to three small joints; 3, *Limulus* has lost the antennae, which the olenellids are known to have had (Dunbar, 1925); and 4, behind the prosoma the chilaria, the appendages of the following segment, the first post-cephalic or abdominal, have advanced so as to close the mouth space behind; whereas nothing of the kind has taken place in the olenellids.

Cephalothorax is therefore a very misleading term, and should be dropped in favour of cephalon. There is no sufficient reason why the arachnids should not walk on their heads; though insects walk on their thorax, and *Homo* walks on his abdomen.

This view of the relation of trilobite to arachnid is in marked contrast with that of Störmer, who homologises the last four cephalic segments of the trilobite with the first four appendage-bearing segments (Ivanov's larval segments) of the Xiphosura (Störmer, 1944, fig. 2, p. 19). This is copied by Vandel in the latest Traité (Grassé, 1949 p. 94, fig. 11). For the comparison both Störmer and Vandel select trilobite protaspids, of *Elliptocephala* and of *Liostracus* respectively, where the development of the two foremost glabella segments is in each case retarded, attributed here to their appendages being enclosed by the hypostome.

Within the Trilobita are exhibited the early stages of the relative reduction of some of the six dorsal head segments, a feature which has characterised most arthropods. It is due to specialisation of these appendages to alimentation, and their consequent reduction, followed by the incorporation of two or three anterior ones within the gut.

In the most *primitive trilobites* the *ratio* of these *six segments of the head* to the *first six segments of the thorax* (averaged over 6 species) is 1:1.

In those primitive families, in which owing probably to a change in the character of the food the glabella expands in front, the cephalic rachis may lengthen; e.g. the ratio in Olenellidae (average of 10 species) is 1.0:0.85; and in Paradoxidae (average of 8 species) is 1.0:0.71.

At the opposite pole from these in some specialised forms the cephalic rachis may diminish, e.g. in *Acidaspis* (average of 11 species) it is 1.0:1.5, leaving out the aber-

rantly short-headed *A. buchi* with ratio 1:2.7.

In modern arthropods comparable measurements are difficult, both because of the lack of dorsal furrows defining a rachis, and because of the change in direction of the axis; hence the whole head must be taken. But the comparison is of interest in view of the claim made above that the primal head in all of them consisted of this same number of segments, together with the parts primitively ventral. These modern classes divide themselves naturally into two contrasted groups; for on the one side we have the Arachnida s.l. that walk on their head limbs, and on the other the classes that do not, e.g. the Crustacea and Hexapoda that walk on thoracid and the Myriapoda that walk on all their body limbs. A very few measures will suffice to bring out the contrast. Unless otherwise indicated, the ratios are between the length of six head segments and six abdominal segments.

Arachnida	
Eurypterus	1.0:1.4
Buthus	1.0:1.6
Scorpio	1.0:2.0
Crustacea (head: 6 thoracic)	
Anaspides tasmaniae	1.0:3.3
Chilopoda	
Scolopendra morsitans	1.0:4.0
Hexapoda (head: 6 abdominal)	
Aptera—*Campodea*	1.0:3.0
Odonata—*Aeschna*	1.0:4.0

If in the Hexapoda we had used the thorax and the first three abdominal segments, the last figure would of course be much higher.

This incorporation of pairs of appendages within the gut indicated in the trilobite had had its parallel previously in the evolution of the polychaet from the primitive annelid, in which evolution it took place three times over. Here indeed it was the study of the trilobite that led to its discovery. In the polychaet the neuromeres also, serving those segmental appendages, because they were ectodermal were likewise carried up the gut; and, because after each invagination the remainder of the central (then lateral) nervous system joined up again directly to the brain, those neuromeres became part of the visceral nervous system (Raw 1949, pp. 10–22). Snodgrass (1938, p. 45) maintained that no homology existed between the visceral nervous system of the annelid and that of the arthropod: the writer has been of that opinion for a much longer time. It is indicated by the fact that the visceral nervous system of the annelid issues from the fore brain, the primal brain, whereas that of the arthropod issues from the tritocerebrum.

As six normal segments+peristome +prostomium are here claimed to have become the head of the arthropod, this constitutes a new theory of the segmentation of the arthropod head, and the representatives of these segments and appendages are to be sought in the head of all the arthropod classes.

This claim of close relationship of all the true arthropods to one another, based on the equivalence of their primitive heads, and also the claim of direct descent of the arthropod from the polychaet are in marked contrast with what is perhaps the latest expressed opinion. According to W. K. Gregory (1950, table 4, p. 169) the Coelenterata gave rise to two separate groups of phyla which include arthropods: the first group includes the Arachnida (s.l. including Merostomata), the Trilobita and the Crustacea, of equal status with one another; the second group derived separately but similarly to the first group, also embraces three, of equal status with one another, namely, the Mollusca, the Annulata (presumably he means Annelida), and the Onychophora, which is represented as giving rise successively to the Myriapoda and the Insecta! The differences between our views are so great, that it would take up too much space to discuss them.

But besides the evolution of the adult (phylogeny), which incidentally has been dealt with, there is the evolution of the development or ontogeny. The latter is divisible into the embryonic and the larval: of the first of these we can perhaps never know anything, but we have learned much of the second, which however there is no occasion here to discuss. It may be remarked however that the larval ontogenies that we know in the trilobites are simple and direct, and lead us to the Arachnida; not at all to the Crustacea, still less to the Insecta.

18. THE CLASS TRILOBITA

Trilobites have usually been classed with the Crustacea; but even before this century their nearer affinities were recognised. They

were grouped by Claus, for example, with the Xiphosura and Eurypterida in a division, "Gigantostraca" of the Crustacea, which however, was followed immediately by the "Arachnida." The proof of this relationship to the Arachnida the writer hopes soon to present. Lankester (1903 and 1910) assigned them to his Arachnida, as a lower grade—his Anomomeristica. Later opinion has tended to remove them again. Borradaile, 1935, makes them a subphylum between the Onychophora and the Crustacea. Störmer on the contrary (1944) again puts them in the Arachnomorpha; but his views could hardly be more different from those of the writer.

The mode of origin of the arthropod classes, as suggested by the trilobites, might well indicate their proper classification. Störmer has lately studied this very subject. He accepts the views of Ivanov: that the Arthropoda are polyphyletic, and that different classes have different numbers of "primary or larval" somites, the Crustacea having two, whereas the chelicerates have four. But he homologises the four *anterior* appendage-bearing somites of the embryo of *Limulus* with the four *posterior* somites of the trilobite's head, and believes that *Limulus* has two or three more somites in its "cephalothorax" (1944, pp. 19, 78, 133 and 135).

He concludes that the Arthropoda have four different origins from the annelids; and the order in which they are placed is: I Myriapoda and Insecta, II Trilobitomorpha and Chelicerata, III Crustacea and IV Pantopoda. To thus widely separate the Myriapoda and Insecta from the Crustacea, and also the Pantopoda from the Chelicerata will hardly meet with approval.

But, surprisingly, the homology of the four anterior appendage-bearing segments of *Limulus* with the four posterior cephalic segments of the trilobite is accepted by A. Vandel in the latest pronouncement (Grassé 1949, p. 94). Seeing that no larval trilobite is known with fewer segments than those of the cephalon, and seeing that every cephalon comprises the hypostome, the rostrum or its equivalent and six dorsal segments, the statement that trilobites have four larval somites is pure fabrication based on an unconfirmed theory respecting *Limulus;* and its application to the larva of the olenellid by Störmer, and that of the ptychoparid by Vandel is in each case quite unjustified.

Though we may know too little as yet, our study of the trilobite strongly suggests that the Arthropoda are monophyletic; and it gives an entirely new basis for that contention. It gives reason for believing: that all the classes have the same fundamental composition of head; one much more comprehensive than is usually believed, consisting of eight elements, of which the first is itself highly complex in origin. It proves conclusively that the head of the trilobite, which exhibits its metamerism so clearly, has exactly the same somitic composition as the "cephalothorax" of the chelicerate; and it offers an entirely different conception of the relationship between the arthropod classes.

If the claim made above is correct, viz. that all arthropods have the same cephalon —the only tagma which they have in common—a reasonable basis of classification is the character of this tagma; and it suggests a classification of the sufficiently known classes into three subphyla:

ARTHROPODA

I. Trilobita: much the most primitive, lying nearer to the origin of all other classes and being besides the most ancient.
II. Chelicerata including Pantopoda: having in general lost only the antennae from its cephalic appendages.
III. Antennata = Mandibulata: having suffered a considerable reduction in the number of cephalic appendages, and having reached a common specialisation to a large degree.

A. Vandel (1949, p. 153) arrives at this subdivision but, as noted above, he has a very different conception as to the status of the trilobite, and even calls them "Proarthropods" in contrast with the other Classes which are his "Euarthropods."

The writer, though he would derive the Chelicerata from a Precambrian trilobite, and claims a very close relationship between them, would still put them in separate classes, because there is no evidence that any trilobite had chelicerae, or that any were without antennae.

19. CONCLUSIONS

This study, limited to the external morphology of the more primitive trilobites, has led to conclusions, so numerous, so revolu-

tionary and, in the writer's view, so significant, that it is advisable to briefly specify them. Here for the sake of completeness the conclusions of the study are presented.

1. Trilobites, by far the most primitive of all known arthropods, are so much nearer to the antecedent non-arthropodan ancestors, that they indicate clearly the origin of the trilobite class.

2. Being so much nearer, also, to the origin of other arthropod classes, than any modern or well preserved fossil forms of these, their study helps greatly in tracing the origin of these classes also.

3. The very close comparisons that one can institute between the trilobites and modern polychaets indicate, indeed, the nature of the polychaet which was ancestral to the arthropods: this is deduced to have combined in itself characters now found in the Eunicidae, the Phyllodocidae and the Polynoidae.

4. The external organs of the arthropod are practically all, except for the compound eye, derived from the polychaet. These include the segments, the eyes and other sense organs, the pleura, and other appendages—ambulatory, natatory, respiratory and sensory.

5. Three definite stages are indicated as coming between the ancestral polychaet on the one hand and the trilobite and higher arthropods on the other. These are named: I, the pro-arthropod, the stage preceding the evolution of the arthropod head; II, the prot-arthropod, furnished only with simple eyes and before the evolution of the compound or radiate eye; III, the deut-arthropod, after the evolution of this last.

6. The pro-arthropod, when adult, was many-segmented, worm-like and benthonic, walking under the protection of a chitinous dorsum, consisting of terga and pleura: terga of the prostomium, peristomium, all normal segments, and of the telson; and pleura on all normal segments. The parapodia had already been differentiated:—the notopodium reduced to a pleuron, largely protective in function, but still moved by muscles and functioning in swimming; the neuropodium into a biramous appendage, serving mainly for ambulation and respiration. The ventral surface of the body and the neuropodial appendages were only weakly sclerotised.

Probably in swimming it would progress like an annelid, by wave motion in the horizontal plane and by waves of motion along its pleura; and in walking, like a centipede by waves of motion of its endopods accompanied by horizontal waves of the body.

7. The head of the trilobite is the same as that of all the other arthropods. It is the only tagma, which all have in common; and it represents the prostomium and the peristomium which were subretroverted, and the succeeding six normal segments of the polychaet and the pro-arthropod. As a consequence to a constant mode of feeding the terga and pleura of these six segments, as well as the ventrally situated prostomium and peristomium coalesced into a cephalon, excepting that a few soft sutures were left, which parted in ecdysis. This was especially necessary at this stage owing to its spinose form. The sutures, the origin of which is deduced, are, in modified form, still traceable in various arthropod classes.

8. This composition of head may have been determined by the polychaet ancestry, for it coincides with the stage of development of the polynoid polychaet when it ends its pelagic existence, and settles on the sea floor.

9. Inheritance from the ancestors of the Polynoidae entailed merocyclism, normal segments 1, 3 and 4 and 6 were macrosomites, and caused the head to be ended by a macrosomite. But the notopodia of the macrosomites were not then elytra, as in that family: they were pleura, larger in size, and with longer spines, which still projected after the formation of the head. This resulted in the head having at first four pairs of spines besides an occipital. When however the adjoining spines on segments 3 and 4 had coalesced into the parial spine, it became "heptacicephalic" with procranidial, parial, and metacranidial pairs of spines besides the occipital. This heptacicephalic form found in certain larvae was claimed in 1924 as ancestral to all trilobites. Very probably it was the dominance of the macrosomites that determined the exact limits of the first benthonic larva of the pro-arthropod, and consequently of the head of the arthropod.

If behind the head, the merocyclism in the prot-arthropod was, as in the Polynoina and Hermionina with diads for some distance and triads beyond, deployment could

produce two groups:—one with only diads behind the head, which might give rise to Diplopoda; another with only triads, ancestral to Arachnida, Crustacea and Hexapoda.

In the higher classes of arthropods the primitive merocyclism was responsible also for determining:—1, the limits of other tagmata, and 2, the nomomerism which especially characterises those classes.

10. The polychaet contributed to the arthropod head a nervous system comprising a complex brain from the prostomium consisting of a paired fore-brain (probably due to an ancient synthesis), next the three consecutive pairs of ganglia of the mid-brain, together with a pair of hind-brain ganglia. These together have come to constitute the procerebrum of the arthropod.

Next comes a pair of ganglia of the peristome, innervating a pair of antennae and now forming the deutocerebrum, followed by six pairs innervating the first six normal segments, the first pair of which was to form the tritocerebrum.

In the polychaet the fore-brain innervated olfactory organs handed on to the arthropod. The mid-brain served two pairs of eyes, which migrated on to the dorsum and are represented by the median eyes of *Limulus*, the nauplius eyes of Crustacea, and the ocelli of insects; it served also several antennae (5, or 3 pairs), all of which are lost.

The peristomial ganglia innervated:—the antennae, which only the chelicerates have lost; a pair of eyes, to migrate on to the hypostome in the trilobite, and to form the "ventral eyes" of *Limulus*, also to migrate on to the dorsum in Arachnida to form their median eyes, and in insects to form the eye-spots in the seven lateral eyes of some larvae.

The ganglia of the six normal segments innervated:—six pairs of appendages, of which only the chelicerate retains them all as external appendages; and six pairs of eyes, extensively lost by the trilobite and the Crustacea, but represented by the lateral eyes of Arachnida, the six similar larval eyes of insects and probably by the adult eyes of some Myriapoda.

Altogether therefore there are three classes of eyes in arthropods inherited from the polychaet through the pro- and prot-arthropod. But all these originally were segmental eyes.

Behind the head the segments were free; each bearing eyes, pleura and appendages; whereas the anal "segment" bore cirri.

11. The chelicerae in the chelicerates were reduced to four, three or two "segments" partly through cover by the labrum; but in other classes various numbers of the anterior members of these six pairs were reduced to apparent loss. Their vestiges, where they still exist are to be sought up the alimentary canal. This constitutes an entirely new theory of the relationship between these arthropod classes.

12. The brain in the prot-arthropod would be housed at first in the labrum; but, with the migration of the prostomial eyes up to the light and on to the dorsum, the brain also migrated; and great changes in the innervation of the labrum and of the dorsal segmental eyes followed, the labrum being *secondarily* innervated by the tritocerebrum and the eyes by the procerebrum.

13. The divergence of the trilobite from the other early arthropods apparently depended on slower locomotion and on their habit of protecting themselves by close apposition of their body to a surface, chiefly that of the sea floor. To this mode of protection various effects can be attributed.

The curtailment of the body length and of the segmentation, common to all the arthropods, is here different in mode; and is in general independent of merocyclism, in contrast with the mode in the higher arthropods.

The dorsum was already protected, and became more so; and as the surface to which the body was applied protected the ventrum, this remained weakly chitinised, whereas the dorsum became even calcified. For, to give further protection, the pleura extended downward to meet that surface; and the combination of this and the curtailment of segmentation effected the semi-ovoid body-form. This entailed loss of the inherited merocyclism; for the pleura and the segments which bore them came to form a graded series from the largest behind the head, diminishing rearward to minute at the rear, where development ceased. The form of pleuron to which this gave rise was the falcate. Later, when in many scions the

advantage of enrolment for protecting the ventrum was appreciated, all the segments, which in the enrolled trilobite opposed the head, became coalesced into a pygidium; and usually to facilitate enrolment the pleural spines of the free segments became truncated, rounded, and facetted; and the pleural spines disappeared.

An important result of this trilobite mode of life was that lateral motion of the segments relative to one another, which had characterised the pro-arthropod, was lost; and their motions became limited to the direction of the median plane.

14. In the evolution of this semi-ovoid body, as claimed already in 1924, 1925 and 1927, the heptacicephalic head had given place to the various plans of head exhibited by trilobites. The mode of life had tended to develop a cephalon of roughly a quarter-sphere resting on or sliding over the substratum, which motion the procranidial and parial spines would have opposed. In different families the adaptation was effected in different ways.

In proparial families (Phacopidae, Cheiruridae etc.) the procranidial and parial aborted, and only the metacranidial survived.

In mesoparial (Beecher's "Opisthoparia") such as the Paradoxidae, the procranidial and metacranidial have disappeared, and the parial have revolved to the posterolateral angles.

In the metaparial family, Olenellidae, both the parial and procranidial have revolved to the posterior border; and the procranidial have carried with them the anterior branches of the facial sutures and the connecting sutures. This extended the rostrum into a semicircular strip, and the rostral suture into a semicircle. In this case the loci of all three pairs of head spines reached the posterior border. This has had two consequences: first, either the procranidial and the parial have coalesced in the genal spine, as in the *Holmia* group (the Holmiinae), or the metacranidial and the parial have coalesced in the intergenal spine, as in some of the *Olenellus* group (the Olenellinae); second, the semicircular rostral suture has entirely replaced the dorsal facial suture for ecdysis, and the shield has ankylosed completely along the facial sutures, as claimed first in 1924.

To a considerable extent the changes above mentioned were effected within the known ontogenies of the trilobites, as described in 1925 and generally accepted.

15. Though previous writers seem all to have believed that the mouth of the trilobite lay above the posterior end of the hypostome, the writer gives reason for the belief that in all primitive forms it lay above the anterior end; and that only later did it migrate rearward, as the anterior appendages, apart from the antennae, became reduced, and enclosed in an extension of the alimentary canal. The same kind of change has taken place in all arthropods except the chelicerates.

16. In the chelicerates the pregenital segment is acknowledged by all authorities to belong to the abdomen. The prosoma without this has exactly the same constitution as the head of the trilobite and in the writer's view as the heads of the other arthropods also; it is not, as authorities still say, a union of head and thorax. "Cephalothorax" should therefore never be used for it, but should be replaced by head or cephalon.

17. The trilobites suggest an answer to the old problem as to whether the arthropods constitute a single phylum. Almost certainly they do.

18. Primitive polychaets now have indefinite and great numbers of segments, often several hundreds; and it was probably so in Precambrian time. The evolution of the arthropod involved the formation of a much more comprehensive head, but a much less comprehensive body, than had the polychaet ancestors. Many paleontologists however have expressed the opposite view —e.g., G. F. Matthew, Beecher, Raymond and lately Störmer, believing that the ontogeny in its building up of segments was repeating the origin of the arthropod. On the contrary, it is the origin of the annelid, that is recapitulated.

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EOCENE CORALLINE ALGAE FROM THE MEGANOS FORMATION, CALIFORNIA

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ABSTRACT—Results of a study of a suite of algal limestones collected by Dr. Joseph J. Graham from the Byron Quadrangle, California. The limestone contains abundant fragments of exceptionally well-preserved coralline algae associated with Foraminifera, Bryozoa, and echinoid spines. The algae include eight species of *Lithothamnion*, four species of *Mesophyllum*, and one *Archaeolithothamnion*. Of these 13 species, five are described as new. They are *Lithothamnion manni*, *L. grahami*, *L. luxurum*, *L. meganosium*, and *Mesophyllum californicum*.

INTRODUCTION

IN 1946, Mr. John F. Mann sent the writer some samples of algal limestone from the Meganos formation. The collection of about 15 specimens is the basis for the present study. The material came from an area then being studied for a graduate thesis by Joseph J. Graham. The authors are grateful to these gentlemen for supplying the material and the stratigraphic information. The Colorado School of Mines provided the thin sections, laboratory facilities, and photographic supplies. The types are in the Johnson Collection at the Colorado School of Mines.

STRATIGRAPHIC SETTING

Mr. Graham kindly supplied the following note on the occurrence of the algal limestone.

The sample which Mr. Mann forwarded to you was from a limestone bed exposed in the northwest-southeast trending elliptical-shaped hill in the Central part SE¼. Sec. 27, T. 1 N., R. 1 E., Byron (California) Quadrangle, aerial photo BUU 268-37. (The north central part of BUU 283-58 that shows this outcrop.) I consider this bed to be Meganos C in age (See Clark and Woodford, Univ. Calif., Publ. Bull. Dept. Geol. Sci., vol. 17, 1927). This is the only occurrence known to me of algal limestone in this unit of the Meganos (in fact, I have never observed it anywhere else in any part of the Meganos). I have seen some Foraminifera in this algal limestone but did not record them because I could not use this locality in my faunal charts.

I am sorry I can give you no ecological information; however Clark and W. discuss the Meganos D fauna in their paper and these fossils occur on the ridge just NE of the algal limestone.

THE ROCK

The limestone is unusual—a rough weathered specimen superficially looks like a piece of weathered granite with the orange algal fragments suggesting feldspar and the enclosed greenish silt suggesting weathered iron silicates. Algal material comprises from 24 to 43 per cent of the specimens studied, averaging about 34.0 per cent. Besides algae, the rock contains appreciable amounts of echinoid spines and plates, Foraminifera, and shell fragments. Table 1 gives the detailed amounts in each slide.

The algal material is unusually well pre-

TABLE 1.—ORGANIC FRAGMENTS IN THE LIMESTONE

Slide number	1134	1135B	1230	1239	1243	1244	1327	1328	1388	1389	Average %
Calcareous red algal	37.5	39.1	34.0	23.6	42.8	30.9	28.2	34.0	34.9	34.3	34.0
Foraminifera	.4	2.6	.6	1.1	.8	4.3	1.4	1.2	.7	2.7	1.6
Echinoids	2.3	4.2	7.9	2.9	1.5	3.8	3.4	4.1	5.3	1.8	3.7
Bryozoans	2.4	4.4	1.7	1.6	1.9	1.4	1.0	1.7	2.2	3.1	2.1
Molluscs	17.4	12.1	12.1	9.7	8.5	6.8	15.3	13.1	13.2	12.7	12.1
Total	60.0	62.4	56.3	38.9	55.5	47.2	49.3	54.1	56.3	54.6	53.5

served and shows structural detail frequently missing in fossil specimens.

PETROLOGY

The specimens examined of the Meganos formation are of a glauconitic, calcareous, algal limestone. Superficially, the limestone has the appearance of a porphyritic granite in a hand specimen. Pink fragments of coralline algal colonies suggest orthoclase fragments consisted of microcrystalline to finely crystalline material. Some medium to coarsely crystalline calcite was observed in molluscan shells, probably the result of reorganization of original aragonite. A number of molluscan valves and foraminiferal tests have retained their original lamellar calcite structure.

The major constituents of the insoluble residue are quartz, feldspar, and glauconite.

TABLE 1.—MEASUREMENTS (IN μ) OF ALGAL SPECIES FROM THE MEGANOS FORMATION

Name	Growth Habit	Hypothallus		Perithallus		Conceptacles	
		L	W	L	W	L	Ht.
Archaeolithothamnion							
A. aff. *keenani* Howe	Crustose	10–21	9–20	10–18	10–19	43–59	94–116
Lithothamnion							
L. manni, n. sp.	Crustose	13–20	6–12	11–17	6–11	355	135
L. grahami, n. sp.	Thin crust	17–29	10–14	9–20	9–12	270–310	150–170
L. sp. A.	Crustose	20–37	10–14	10–17	7–12	Unknown	
L. luxum, n. sp.	Nodular crust			14–17	7–10	200–270	100–115
L. aff. *validum* Foslie	Nodular crust	10–22	5–9	5–11	9–12	210–700	100–150
L. meganosium, n. sp.	Crust with mamelons	Poor or absent		7–14	6–9	350–500	170–210
L. wallisium J. & Tafur	Crust with mamelons	11–20	8–12	11–22	8–14	250–410	99–130
L. cf. *laminosum* Howe	Thin crust	9–21	7–12	10–13	9–14	Absent	
Mesophyllum							
M. schenki Howe	Mammalated crust			8–14	6–11	330–350	109–130
M. cf. *obsitum* Airoldi	Thin crust	7–26	6–12	5–12	5–9	164–200	72–90
M. cf. *fructiferum* Airoldi	Thin crust	12–19	6–8	6–10	9–11	420–450	183–210
M. californicum, n. sp.	Branching	9–17	8–12	12–25	10–15	325–365	130–150

phenocrysts in a finer groundmass. The presence of angular, detrital quartz grains in the matrix furthers the deception, and numerous darkened grains of glauconite substituting for an accessory mafic mineral complete the illusion.

MINERALOGY

The principal constituent mineral is calcite. Eighty per cent of the rock by weight is acid soluble. Calcite is in excess of 79 per cent, with less than one per cent fibrous aragonite in a few molluscan shells. No dolomite or other acid soluble mineral was detected.

Considerable textural variation was observed in the calcite. The bulk of this mineral, of the cryptocrystalline variety, was contained in the structure of the algal colonies. The groundmass around the colony

Quartz and feldspar fragments were in about the same abundance, each representing about 35 per cent by volume of the insoluble. The grains of these detrital minerals were small and angular with no evidence of rounding. The quartz grains were clear, without frosting, and optically strained. The feldspar minerals are orthoclase and oligoclase with a small amount of andesine and an occasional grain of microperthite.

The most distinctive constituent of the insol is glauconite, making up 20 per cent of the residue. The glauconite grains were for the most part, flattened elliptical pellets or ellipsoids, with an irregular fracture pattern when seen in this section. A few grains had a pleated accordion appearance with distinct traces of original mica cleavage.

Some clay, about eight per cent, is present in the insol. Stain tests indicate kaolin-

ite is the principal clay mineral with a trace of montmorillonite.

The miscellaneous members of the residue, about 2%, are green and brown mica and a few grains of detrital chalcedony. Most of the mica is green biotite, of incipient glauconitization. A few flakes had both green and brown mica in distinct zones. Rarely an unaltered flake of pure brown biotite was found.

ENVIRONMENT OF DEPOSITION

The petrographic features of the Meganos limestone suggest that it was deposited in a warm, saline lagoon enclosed on the seaward side by a headland or a fringing or barrier reef of coralline algae. The specimens examined appear to be from the close backreef area. The greater bulk of the rock is composed of rudely stratified fragments of algal colonies broken and washed into the backreef area by wave action. The interstices between algal fragments are filled with microcrystalline to finely crystalline calcite which contains the previously listed insoluble minerals. The abundance of broken algal colonies suggests near reef deposition in a calcareous ooze, now recrystallized, which accumulated in the quiet lagoon. The warm nature of the environment is supported by the luxuriant algal growth. The abundance of glauconite confirms this and postulates a quiet, saline condition.

The clues concerning the nature of the adjacent landmass are found in the insoluble residue. A low, semi-arid expanse of metamorphic rocks with a few intrusives is visualized as the source area for the detritals. The crystalline nature of the hinterland is evidenced by the abundance of glauconite, representing original biotite derived from schistose rocks. The quartz grains are predominately optically strained, substantiating a metamorphic source area. An occasional grain of microperthite implies a few intrusives.

Long mechanical weathering is evidenced by the angular nature and smallness of the quartz and feldspar grains. Lack of alteration of the feldspars and the small percentage of clay minerals are indicative of the small degree of chemical weathering of the source rocks. This adds up to an arid or semi-arid land area. The low elevation of this coastal area is strictly hypothetical. The quartz and feldspar grains are small and there is no rounding shown by any detrital grains. They were carried a short distance before deposition, yet they are quite small and must have been broken to this size by mechanical weathering before transport. Had the source area been rugged and high, a residual blanket of uniformly sized, mechanically broken material would not be likely to accumulate and some outsized detrital grains would have been present in the insoluble residue. This conclusion is admittedly shaky. An alternate hypothesis of deposition far offshore is possible, so that only the finely classified detrital sediments were deposited in the lagoon or close backreef area.

CLASSIFICATION OF CORALLINE ALGAE

The classification based on Lemoine (1939, pp. 38–39) is used:

Class RHODOPHYTA
Family CORALLINACEAE
Subfamilies:
A. MELOBESIEAE
Archaeolithothamnion
Mesophyllum
Lithophyllum
Melobesia
Lithothamnion

EXPLANATION OF PLATE 15

FIG. *1*—*Lithothamnion* sp. A, ×25. A general view of the tissue showing hypothallus, perithallus and several secondary hypothalli developed around injured areas. (p. 134)
2, 3—*Archaeolithothamnion* aff. *keenani* Howe, ×125. Tissue and rows of sporangia. (p. 133)
4—*Lithothamnion manni* n. sp., ×75. Tissue including hypothallus, perithallus and a conceptacle. (p. 133)
5— *Lithothamnion grahami* n. sp., ×75. Hypothallus at base, perithallus and one conceptacle space. (p. 133)
6—*Lithothamnion* aff. *validum* Foslie, ×25. Section through a nodular encrustation growing around a fragment of a fossil. Note numerous wide, low conceptacles. (p. 134)

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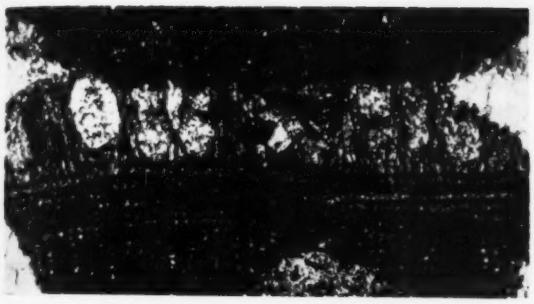

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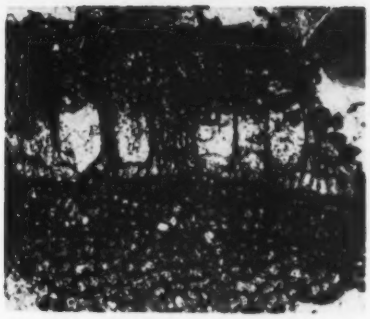

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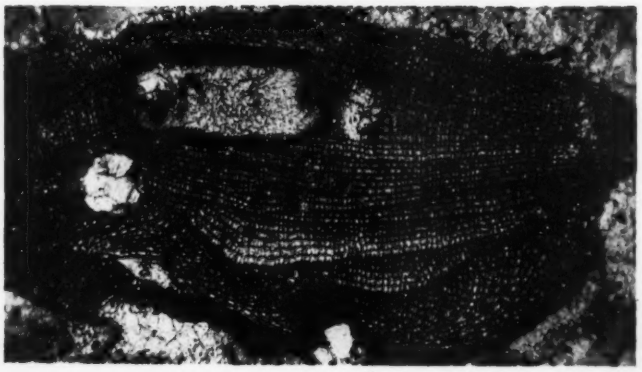

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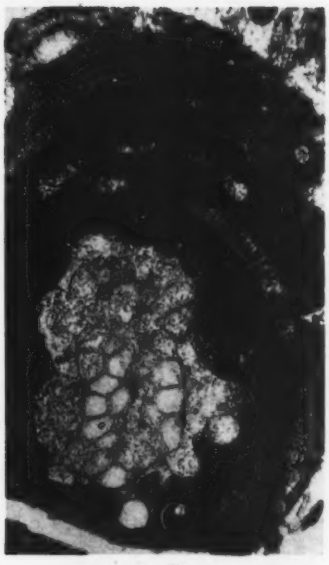

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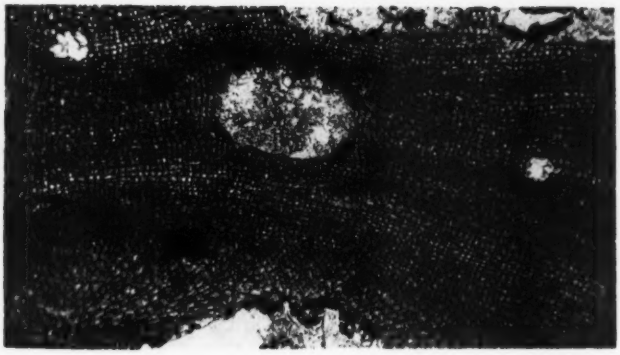

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Johnson and Stewart, California Eocene algae

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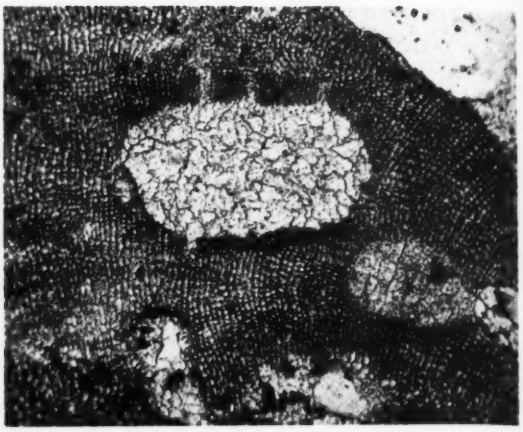

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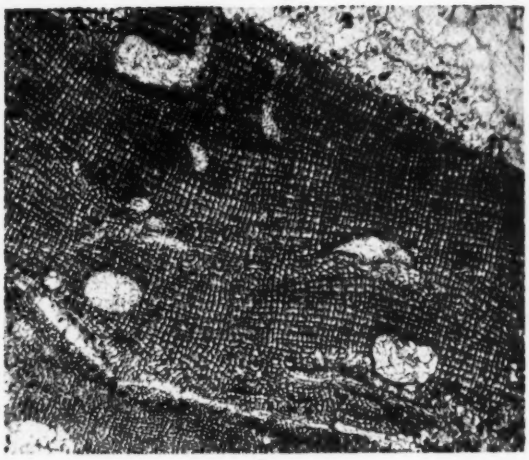

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Johnson and Stewart, California Eocene algae

DESCRIPTION OF THE ALGAE

Subfamily MELOBESIEAE

Genus ARCHAEOLITHOTHAMNION Rothpletz

This genus is most interesting to the paleobotanist. It has a long fossil record and a known range extending from the Jurassic to the present. It appears to have reached its zenith during the Eocene. Its simple but rather spectacular structure with rows of sporangia within the tissue insures easy recognition. In this collection, it is represented only by one species.

ARCHAEOLITHOTHAMNION aff. A. KEENANI Howe

Plate 15, figures 2, 3

Description.—Thallus forms a crust 0.6 to 0.7 mm. thick. Hypothallus poorly developed, consisting of a few curving rows of irregularly rectangular cells measuring 10 to 21 μ wide and 9 to 20μ high. Perithallus tissue fairly regular with the horizontal rows more strongly defined than the vertical. Cells rectangular measuring 10 to 18μ wide and 10 to 19μ high. Spore cases elliptical, arranged in regular rows, becoming overgrown and imbedded in the tissue, measure 94 to 116μ high and 43 to 59μ wide.

Remarks.—This species was represented only by two small fragments. The general appearance and cell dimensions closely fit Howe's description (1934, p. 513). The spore cases are slightly longer than in the type.

Genus LITHOTHAMNION Philippi

This genus is characterized by a tissue consisting of hypothallus and perithallus and large conceptacles with many apertures in the roof. It has a known time range from the Cretaceous to the present. Today it develops in many growth forms and did the same during the geologic past. The encrusting, lamellar, and foliate forms are common as well as larger mamillate and branching forms. Unfortunately, very little work has been done on these thin types, even in the modern floras. As a result, it is difficult to interpret such fossil forms and to compare them with modern species.

Lithothamnion is abundantly represented in this collection both by individuals and species.

LITHOTHAMNION MANNI Johnson & Stewart, n. sp.

Plate 15, figure 4

Description.—Thallus crustose, consisting of a well-developed plumose hypothallus and a moderately thick perithallus. Hypothallus of curved rows of long, slightly rounded cells, 13–20μ long and 6 to 12μ wide. Perithallus consists of quite regular rows of rectangular cells 11 to 17μ high and 6 to 11μ wide. Perithallus shows pronounced, irregular, probably lenticular growth zones.

Conceptacle: Length 355μ, 135μ high.

Remarks.—In cell dimensions this species differs considerably from all previously described Eocene and Oligocene species. The most conspicuous feature is the well developed plumy hypothallus.

Type.—Slide #1229 Johnson collection —Colorado School of Mines.

LITHOTHAMNION GRAHAMI Johnson & Stewart, n. sp.

Plate 15, figure 5

Thallus forms thin crusts. Hypothallus moderately well developed, consisting of eight to 16 curved rows of cells. Cells rectangular 17–29μ×10–14μ. Perithallus of quite regular cell rows. Cells square 9–12μ, or elongated 9–20×9–12μ. Conceptacles 270–310μ in diameter, 150–170μ high.

Remarks.—Cell dimensions and the relatively high conceptacles distinguish this from previously described Eocene species.

Type.—Slide #1392 Johnson Collection.

EXPLANATION OF PLATE 16

FIG. *1—Lithothamnion wallisium* Johnson & Tafur, ×75. Detail of tissue and conceptacles. (p. 134)

2—Lithothamnion meganosium n. sp., ×100. Detail of tissue and conceptacle showing a number of roof aperatures for escape of spores. (p. 134)

3—Lithothamnion cf. *laminosum* Howe, ×75. Detail of tissue showing narrow hypothallus at base and perithallus above. (p. 135)

4—Mesophyllum cf. *fructiferum* Airoldi, ×75. Portion of tissue showing pronounced growth zones and two conceptacles. (p. 136)

5—Lithothamnion luxurum n. sp., ×40. General view of a section through the colony conceptacles, some of which still show outlines of the contained sporangia. (p. 134)

LITHOTHAMNION sp. A
Plate 15, figure 1

Thallus crustose forming irregular crusts or nodular masses. Both hypothallus and perithallus well developed. The several specimens studied seem to have been injured, probably by animals and had developed a secondary hypothallus as local scar tissue over the injury (well shown in figure 1 of plate 15).

Hypothallus consists of eight to 25 curved rows of rectangular cells which measure 20 to 37μ wide and 10–14μ high. Perithallus built of irregular rows of square to rectangular cells measuring 10–17 (22)μ long and 7–12μ high. Conceptacles unknown.

Remarks.—Represented by several sterile specimens in the collection. In growth habit and cell dimensions, it somewhat suggests *L. abradi* described by Lemoine (1939) from the Eocene of the Mediterranean region. The cell dimensions also are about the same as those of the modern *L. australe* Foslie from the coast of Mexico. In the absence of conceptacles, it does not seem wise to attempt to name it.

LITHOTHAMNION LUXURUM
Johnson & Stewart, n. sp.
Plate 16, figure 5

Thallus develops a nodular crust. Hypothallus well developed with curved rows of cells. Unfortunately, the section studied cuts the hypothallus obliquely so true cell measurements cannot be obtained. Perithallus has a somewhat zoned appearance. Cells rectangular 14–17×7–10μ. Conceptacles abundant, wide and flattened, measuring 200 to 270μ×100 to 115μ. Sporangia 16 to 28μ wide.

Remarks.—Represented by one specimen and several fragments, none of which permit measurement of hypothallic cells.

LITHOTHAMNION aff. L. VALIDUM Foslie
Plate 15, figure 6

Thallus excrusting forming nodular masses around fragments of organic debris. Hypothallus thin but clearly developed, consisting of five to 11 curved cell rows. Cells measure 10–12μ×5–9μ. Perithallus tissue has a zoned appearance but is quite regularly developed. Cells 5–11μ×9–12μ. Conceptacles numerous and unusually wide. Diameter 210 to 700μ and 100 to 150μ high.

Remarks.—This species closely resembles the modern *Lithothamnion validum* Foslie common along the Pacific coast of subtropical North America. It agrees in growth habit, general appearance and in the possession of large, wide, flat conceptacles. It differs slightly in cell dimensions.

LITHOTHAMNION MEGANOSIUM
Johnson & Stewart, n. sp.
Plate 16, figure 2; plate 17, figure 2

Description.—Thallus crustose with mamelons and possibly short, thick branches. The crust varies considerably and abruptly in thickness. Hypothallus very thin or missing. Tissue consists of rows of rectangular cells measuring 7 to 14μ high and 6 to 9μ wide. Horizontal partitions between rows more pronounced than the vertical partitions between the cells. The tissue shows strong growth zones.

Conceptacles 350 to 500μ wide and 170–210μ high, with multiple openings in the roof. Six such openings are clearly shown on the specimen.

Remarks.—The appearance, growth habit, dimensions of the cells and of the conceptacle are very close to *L. Bofilli* described by Lemoine from the middle Eocene of Spain. It differs from *L. Bofilli* in the absence of poor development of the hypothallus which is strongly developed on the type where it forms at least half of the tissue. A careful study of three specimens of *L. meganosium* shows the hypothallus to be absent. It is barely suggested on a fourth.

Figured specimens.—Slides #1327 and 1243, Johnson Collection, Colorado School of Mines.

LITHOTHAMNION WALLISIUM
Johnson and Tafur
Plate 16, figure 1

Description.—Thallus crustose possibly developing mamillary protuberances. Hypothallus moderately developed consisting of curved rows of rounded to rectangular cells. Cells measure 11–20μ long ×8–12μ wide. Perithallus shows numerous irregular growth zones. These zones are more or less lenticular and are formed of four to nine layers of rectangular cells. Cells 11–22μ long and 8–14μ wide. Conceptacles become wide and flat with diameters of 250 to 410μ and heights of 99 to 130μ.

Remarks.—In appearance, growth habit and dimensions of cells and conceptacles

this agrees with the species recently described by Johnson and Tafur (1952) from the Eocene Atascadero limestone of Peru. It closely resembles *Lithothamnion isthmi* Howe from the Oligocene of Panama.

LITHOTHAMNION cf. L. LAMINOSUM Howe
Plate 16, figure 3

Description.—Thallus thin, several superimposed thalli form a thin crust. Hypothallus consisting of two to eight curved or irregular rows of rounded to rectangular cells, which measure 9–21μ×7–12μ. Perithallus composed of fairly regular rows of cells, four to 12 rows thick. Cells rectangular, 10–13μ ×9–14μ. Conceptacles absent.

Remarks.—The appearance, growth habit and cell dimensions of this form agree with Howe's description and illustrations (1934, p. 513, plate 55). It differs only in having a slightly better development of the hypothallus and somewhat longer cells in the hypothallus.

Genus MESOPHYLLUM Lemoine 1928

Characterized by a clearly stratified, zonate branch tissue similar to the genus *Lithophyllum* but having conceptacles with multiple openings similar to the genus *Lithothamnion*. Usually the branches consist largely or entirely of medullary hypothallus with little or no marginal perithallus, which is usually well developed on a typical branching *Lithophyllum*. The genus is represented in the collection by several species and numerous individuals.

Conceptacles frequently rather large and abundant, so in sections of the plant they often appear to occupy a large percentage of the area.

MESOPHYLLUM SCHENKI Howe
Plate 17, figure 1

Mesophyllus Schenckii, HOWE 1934, p. 512, pls. 52, 53.

Description.—Thallus: specimen consists of one mamelon 586μ in length and 486μ in diameter. The tissue is strongly zoned with the individual laminae varying much in thickness and having a typical crescentic longitudinal section. The laminae are roughly concentric though distorted by numerous conceptacles. The individual medullary perithallus cells are subquadrate in longitudinal section measuring 8 to 14μ long and 6 to 11μ high. No basal or medullary hypothallus tissue is apparent. There is a small amount of secondary hypothallus tissue, possibly scar tissue, filling in pits which may represent old injuries.

There are numerous conceptacles 330 to 350μ in diameter and 109 to 130μ high. There are suggestions of as many as six plural openings in the roof of some of the conceptacles.

Remarks.—The general laminate-zonate appearance of the tissue, the subquadrate form of the cells, and the dimensions of the conceptacles, are similar to Howe's description of the type species from the Eocene Sierra Blanca limestone of California. The pits filled with secondary hypothallus tissue are possibly analogous to the lacunae of the original description. The dimensions of the cells in the perithallium are slightly larger than the type. Howe's description, made from numerous specimens is much more complete than ours made from a single mamelon. The section is exceptionally good, however, for the development of conceptacles. Apparently it cuts the conceptacles at near the maximum diameter. As a result, the diameters range from 10 to 30μ larger than Howe's maximum.

MESOPHYLLUM cf. M. OBSITUM Airoldi
Plate 17, figure 5

Mesophyllum obsitum Airoldi 1932, p. 78.

Description.—Thallus is a thin, tight crust varying from 76 to 360μ in thickness and consisting of a distinct, but poorly developed hypothallus, and well-developed, weakly zoned perithallus. The hypothallus is thin and plumose with a few curving rows of elongate, slightly elliptical cells measuring from 7 to 26μ long and 6 to 12μ high. The hypothallus grows tightly on the surface encrusted by the colony. The illustration shows a colony growing on a mollusc fragment with some penetration of the shell surface by hypothallus tissue. The perithallus is composed of rows of rectangular to nearly square cells 5 to 9μ long by 5 to 12μ wide. The cell rows are much distorted by numerous, closely spaced conceptacles and are grouped into faint but definite zones.

Although the thallus forms a relatively thin crust, it contains a large number of conceptacles, tightly grouped together. These measure from 164 to 200μ wide and 72 to 90μ high. As shown in the illustration, some of the conceptacles were formed just

above the hypothallus in the early growth stages, others are scattered throughout the perithallus, and at least two open onto the surface of the colony.

MESOPHYLLUM cf. M. FRUCTIFERUM Airoldi
Plate 16, figure 4

Mesophyllum fructiferum, Airoldi 1932, pp. 76–77, pl. 12, fig. 1.

Description.—Thallus is a thin crust measuring from 372 to 481μ in thickness, with thick, stubby branches 1950μ wide by 2240μ high. The hypothallus is poorly developed with a few slightly curving rows of cells. The perithallus is well developed with the tissue strongly zoned. The zoning is particularly marked in the branches where the individual layers, separated by prominent growth lines, are subconcentric in pattern and crescentic in section. The cells in the hypothallus are elongate and elliptical, measuring 12 to 19μ in width and 6 to 8μ in height. In the perithallus tissue the cells vary from 6 to 10μ wide and 9 to 11μ high; those in the crust being subquadrate with slightly rounded corners, the tissue appearing distinctly rectilinear; while those in the branches are more rounded, the tissue being more irregular. The conceptacles are carried in the outer zones of the branches and are 421 to 453μ wide by 183 to 210μ wide. There are suggestions of as many as six plural openings in the roofs of the conceptacles.

MESOPHYLLUM CALIFORNICUM
Johnson & Stewart, n. sp.
Plate 17, figure 4

Description.—Fragments of a branching form. Branches long and swelling toward the tips. Medullary hypothallus well developed with lenticular (concentric) zones, each composed of five to eight layers of cells. Cells measure 8–12×9–17μ. Perithallus consists of nine to 12 layers of rectangular cells measuring 12 to 25×10–15μ. Conceptacles 325 to 365μ in diameter and 130 to 150μ high.

Remarks.—This species is represented by several fragments of branches. It is closely related to *M. peruvianum* Johnson and Tafur, but has shorter, thicker branches and has smaller cells. It also resembles *M. vaughanii* (Howe) Lemoine, but differs in cell dimensions and slightly in shape of branches.

Genus LITHOPHYLLUM Philippi

Description.—Characterized by well defined hypothallus and perithallus, Hypothallus usually shows a subaxial structure. Branches have well developed medullary hypothallus and marginal perithallus. Conceptacles usually strongly arched with a single large opening at the apex.

This genus is only sparingly represented in this collection by small fragments, which do not supply adequate data to permit valid description.

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EXPLANATION OF PLATE 17

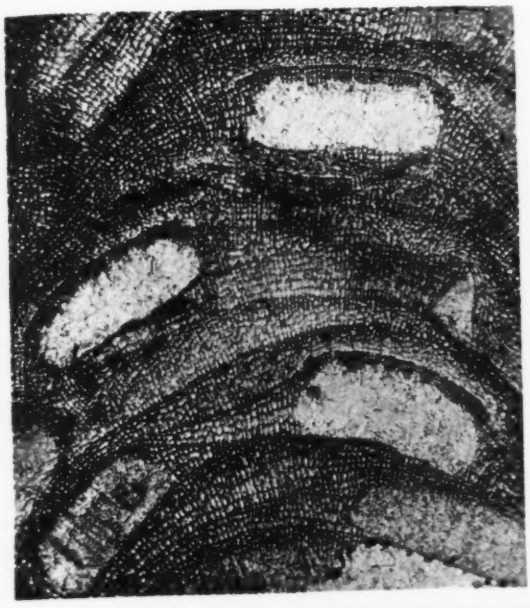
FIG. *1—Mesophyllum schencki* Howe, ×75. Detail of tissue showing strong growth zones and numerous conceptacles with plural roof openings. (p. 135)

2—Lithothamnion meganosium n. sp., ×100. Detail of a portion of the perithallus tissue and space formerly occupied by a conceptacle with numerous openings. (p. 134)

3—Meganos limestone, hand specimen (×1). The light colored areas are algal fragments. (p. 130)

4—Mesophyllum californicum n. sp., ×75. View of a part of the thallus showing strongly zoned central medullary hypothallus, narrow outer perithallus, and several conceptacles. (p. 136)

5—Mesophyllum cf. *obsitum* Airoldi, ×75. General view showing poorly developed basal hypothallus, the perithallus and several conceptacles. (p. 135)



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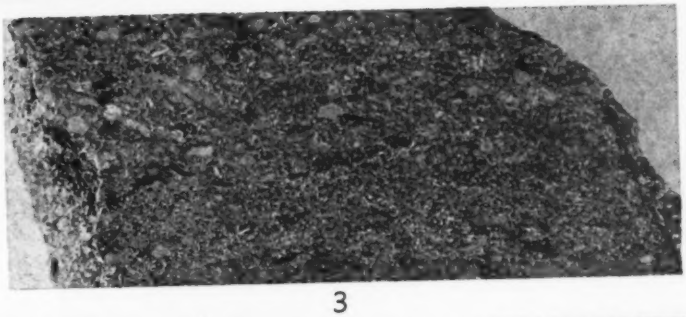

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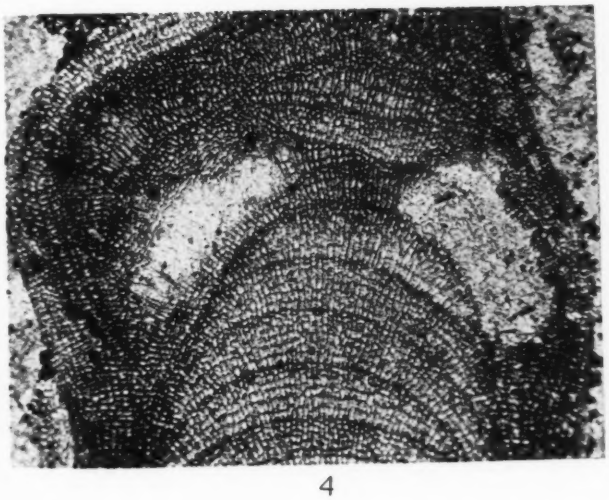

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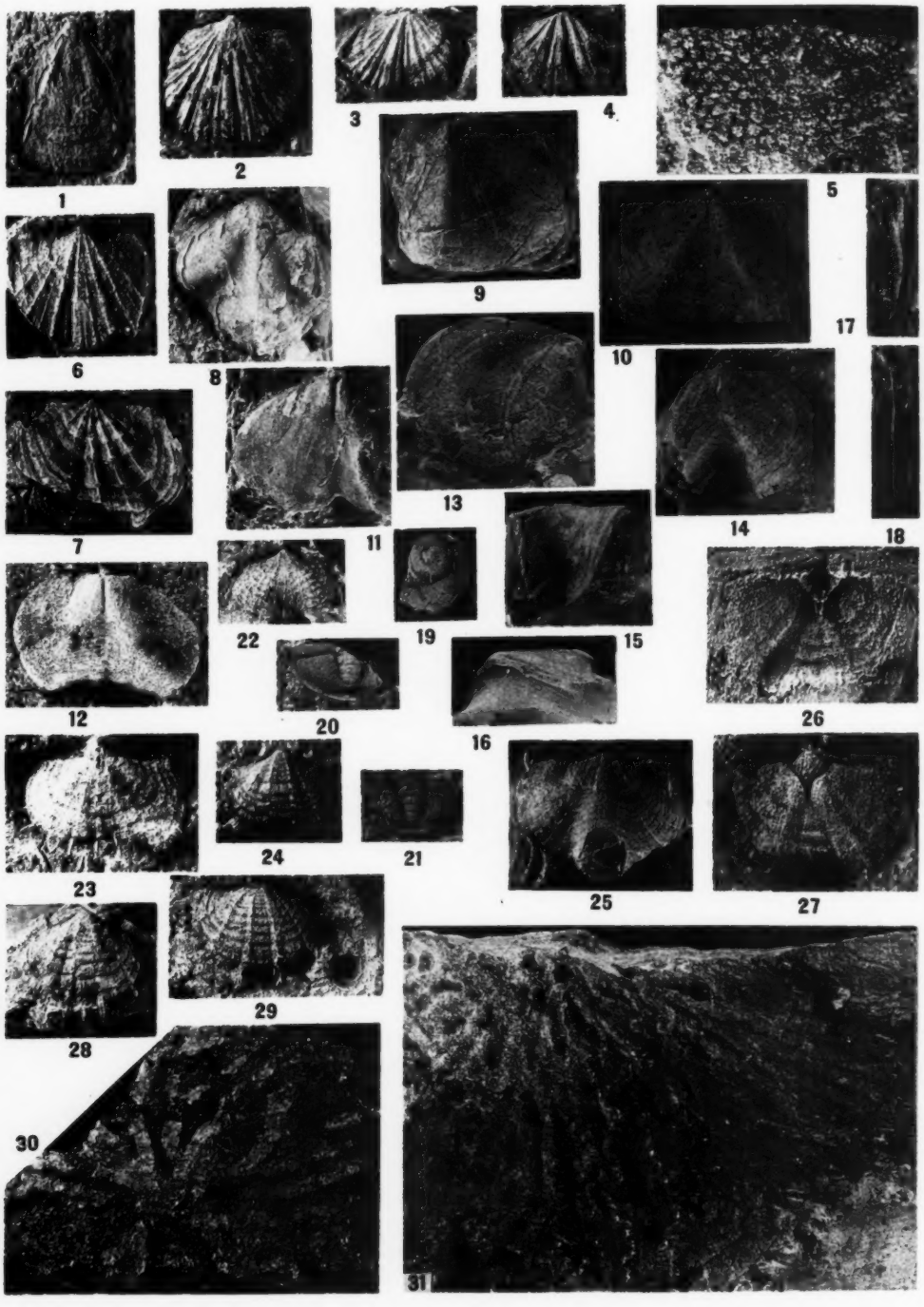
Johnson and Stewart, California Eocene algae



Shaw, Vermont Cambrian fossils

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, PP. 137–146, PL. 18, 2 TEXT FIGS., JANUARY 1953

PALEONTOLOGY OF NORTHWESTERN VERMONT III. MISCELLANEOUS CAMBRIAN FOSSILS

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ABSTRACT—Description of the upper Gorge formation fauna is completed, except for the inarticulate brachiopods, and a summary of the entire fauna indicates that it should be correlated with the Upper Cambrian *Hungaia magnifica* zone. The fauna was dominated by brachiopods although the trilobite remains are the most numerous because of molting.

New species described: *Glyptotrophia spinosa*, *Lingulella? stonei*, and *Serpulites acus*. Unidentified species of *Apheoörthis*, *Orthis*, *Dirhachopea*, and "*Heteronema*" are present in the upper Gorge fauna. The brachiopod homonym *Lingulella vermontensis* Ulrich and Cooper, 1938, not Howell, 1937, is replaced by *L. cooperi*, and the trilobite genus *Lévisaspis* Rasetti, 1943, is suppressed as synonymous with *Hardyoides* Kobayashi, 1938.

INTRODUCTION

THE purpose of this paper is to describe a few miscellaneous fossils from the Cambrian of northwestern Vermont. This unsystematic treatment may be justified by the need for describing and naming several species that are to be discussed in other forthcoming papers. Five brachiopods, a

EXPLANATION OF PLATE 18

Figures 2–31 from negatives made at the United States National Museum under the direction of Dr. G. Arthur Cooper. Specimens 2–31 from upper Gorge formation in north wall of gorge at Highgate Falls, Vermont (Loc. SA-NE-24).

FIG. *1—Lingulella? stonei* Shaw, n. sp. Holotype ventral valve, ×2. MCZ 9346. Collected 130 feet above base of Skeels Corners formation, in road cut 1.77 miles S 11½° E of Bench Mark 259, Georgia Plains, Vermont (Loc. M-NC-3). (p. 141)

2, 3—Archaeorthis crassa Ulrich & Cooper, 1938. *2*, Ventral valve, ×4. *3*, Dorsal valve, ×4. USNM 116613. (p. 139)

4—Orthis sp. Small ventral valve, ×4. USNM 116614. (p. 142)

5—"Heteronema" sp. Unique fragment of zoarium, ×10. USNM 116620. (p. 144)

6, 7— Apheoorthis? sp. indet. *6*, Crushed valve, ×4. USNM 116615a. *7*, Distorted valve assigned to genus, ×2. USNM 116615b. (p. 142)

8–16—Syntrophina carinifera Ulrich & Cooper, 1936, *8*, Dorsal valve, partly exfoliated, ×2. USNM 116616f. *9*, *13*, Dorsal and lateral views of exfoliated dorsal valve showing pallial trunks, ×3. USNM 116616e. *10*, Ventral valve, ×2. USNM 116616a. *11*, Interior of ventral valve showing median septum and spondylium, ×3. USNM 116616d. *12*, Interior of ventral valve showing median septum and spondylium, ×2. USNM 16616b. *14–16*, Ventral, anterior, and lateral views of ventral valve with deep, carinate sulcus characteristic of species, ×2. USNM 16616c. (p. 142)

17, 18—Serpulites acus Shaw, n. sp. *17*, Holotype, ×2. USNM 116621. *18*, Paratype, ×2. USNM 116622a. (p. 145)

19–Dirhachopea sp. Unique conch, ×5. USNM 116619. (p. 144)

20, 21—Hardyoides glabrus (Shaw), 1951. Two pygidia assigned to the species, ×5. USNM 116624b and 116624a, respectively. (p. 145)

22–29—Glyptotrophia spinosa Shaw, n. sp. *22*, Immature ventral valve, ×2. USNM 116617a. *23*, Mature sulcate ventral valve with well preserved rib-spines, ×2. USNM 11617b. *24*, Immature dorsal with prominent rib-spine bases and well developed "frills," ×4. USNM 11617c. *25*, Mature dorsal valve, ×2. USNM 116617d. *26*, *27*, Natural mold of ventral valve with spondylium and median septum, and rubber squeeze of same, ×5. USNM 116617e and Univ. Wyoming IT-137. *28*, Holotype ventral with well preserved rib-spines and exceptionally long frills on margin, ×2. USNM 116618. *29*, Spinose immature dorsal with the fold undeveloped. Associated natural mold of pygidium of *Geragnostus* (*Micragnostus*) *bisectus* (Matthew), 1892, ×4. USNM 116617f. (p. 143)

30, 31—Dictyonema vermontense Ruedemann, 1947? *30*, Best-preserved rhabdosome, ×3. *31*, Large fragment of rhabdosome, ×3. USNM 116623. (p. 145)

graptolite, a bryozoan, a gastropod, and a new species of *Serpulites* from the upper part of the Gorge formation (late Trempealeauian) are included, as well as a new inarticulate brachiopod, valuable in the recognition of the Skeels Corners formation (Dresbachian). The trilobites *Hardyoides glabrus* (Shaw), 1951, and *"Terranovella" gelasinata* Shaw, 1951, are also discussed.

All of the species, except the inarticulate brachiopod, *Lingulella? stonei*, are from a single quarry in the upper Gorge formation. The trilobite fauna of this locality, which lies in the north wall of the gorge of the Missisquoi River at Highgate Falls, Vermont, has already been described (Shaw, 1951). The quarry itself, which has been given the field number SA-NE-24, was first located by Dr. C. H. Kindle (1936, p. 386). It lies approximately 20 feet above the point where the trace of the Highgate Falls thrust reaches the floor of the gorge.

ACKNOWLEDGEMENTS

I am deeply indebted to Dr. G. Arthur Cooper, who kindly arranged for most of the photographs shown on the accompanying plate to be made at the U. S. National Museum, and who reviewed and criticized the completed manuscript; to Miss Diane Crawford my appreciation for her assistance in preparing the final draft for publication.

I also wish to thank Mr. S. W. Stone, who has for the past few years been studying the Milton quadrangle, Vermont, for permitting me to discuss the "Milton dolomite" fauna, which was collected within his area of mapping. And to Dr. C. H. Kindle go my reiterated thanks for permitting me to describe the upper Gorge fauna.

COMPOSITION OF THE UPPER GORGE FAUNA

With this note, all species from the upper Gorge formation, save the inarticulate brachiopods, which are not numerous, will have been described, so it may not be amiss to record the abundance of the various species. This has been done in Table 1, but the raw data given do not convey the true picture of the fauna because the brachiopods, which had two valves, and the trilobites, which molted, have left a record in excess of their actual numerical strength.

To reduce the brachiopods to their proper standing we may safely take the number of specimens of one valve, but the trilobites present a more difficult problem. First, no one knows how many times a trilobite molted, and even if we knew for one species, the figure is almost certainly not the same for all species or even for all individuals in the same species. Second, as has been pointed out before (Shaw, 1951, pp. 98–99) the trilobite remains in this fauna appear to have been subjected to the selective introduction of the more convex parts of the test. Third, there is in this faunule a dearth of fully matured specimens of some species, apparently because of their destruction before burial.

Thus, with full realization of their tentative nature we may make the following *very* provisional estimates:

(1) If we choose *Plicatolina kindlei* as typical of the larger, non-agnostidean trilobites and allow five protaspid molts, plus one for each of the 16 known thoracic segments (Shaw, 1951, pl. 22, fig. 16) plus ten more for the missing segments and holaspid molt stages, we arrive at about 30 molt stages for this species.

(2) By loose analogy of structure, we may guess at approximately the same number for *Parabolinella triarthroides* and *"Terranovella" gelasinata*.

(3) *Missisquoia typicalis*, *Symphysurina minima*, and *Hardyoides glabrus* all must have had shorter thoraces; eleven is the typical number for phacopids, eight to ten for asaphids, and between nine and five for *Norwoodüds*. Using the lesser number of thoracic molts, we arrive at about 25, 25, and 20 molt stages, respectively.

(4) The agnostids may be estimated to have had about a dozen molt stages, mostly devoted to protaspid and holaspid growth.

(5) No protaspids have been recovered for any of the species, but early meraspids are known from cranidia and a few pygidia. Thus, our sample represents none of the earlier stages included in the estimates above. Therefore, we may arbitrarily reduce our factor by five, the number of protaspid molts allowed for each species.

Another complicating factor is the scarcity of large specimens. For *Symphysurina minima* the first 24 cranidia range gradually in length from 0.8 mm. to 15.5 mm., but the

next is about 21.8 mm. long. In *Plicatolina kindlei* the bulk of the cranidia range from 1.4 mm. to 5.5 mm. in length, but the holotype is about 16 mm. long, allowing for restoration of missing parts. The gap is less noticeable in the cases of *Parabolinella triarthroides* (22), *Plicatolina kindlei* (21), *Missisquoia typicalis* (20), *Symphysurina minima* (16), *Hardyoides glabrus* (15), and all others (7). For ease of calculation let us say that each of the first four species is represented by 20 molt stages, *S. minima* and *H. glabrus* by 15, and the remainder by seven.

TABLE 1—SPECIMEN COUNT FROM THE UPPER GORGE FAUNA AT LOCALITY SA-NE-24, EXCLUDING INARTICULATE BRACHIOPODS

TRILOBITES	CRANIDIA	PYGIDIA	FREE CHEEKS	HYPOSTOMATA
Hardyoides glabrus (Shaw), 1951	21	2	1	0
Missisquoia typicalis Shaw, 1951	61	23	0	0
Parabolinella triarthroides Harrington, 1938	56	15	0	0
Plicatolina kindlei Shaw, 1951	21	0	0	8
Symphysurina minima Shaw, 1951	42	32	8	5
"Terranovella" gelasinata Shaw, 1951	36	0	4	0
Geragnostus bisectus (Matthew), 1892	0	28	0	0
G. bisectus var. *typica* Shaw, 1951	15	0	0	0
G. bisectus var. *brevis* Shaw, 1951	5	0	0	0
Pseudagnostus araneavelatus Shaw, 1951	19	12	0	0
P. bilobus Shaw, 1951	15	11	0	0
Homagnostus sp.	5	1	0	0
Litagnostus raymondi Shaw, 1951	10 SHIELDS		0	0

BRACHIOPODS	DORSALS	VENTRALS
Archaeorthis crassa Ulrich and Cooper, 1938	56	78
Glyptotrophia spinosa Shaw, n. sp.	40	51
Syntrophina carinifera Ulrich and Cooper, 1936	15	12
Apheoörthis sp.	2 SPECIMENS	
Orthis sp.	1 SPECIMEN	

MISCELLANEOUS	SPECIMENS
Serpulites acus Shaw, n. sp.	5 TUBES
"Heteronema" sp.	1 ZOARIUM
Dirachopea sp.	1 SHELL
Dictyonema vermontensis Ruedemann, 1947?	8 RHABDOSOMES

After all of this manipulation we have the following estimates of the number of molt stages of each species represented in our fauna: *"Terranovella" gelasinata* and *Parabolinella triarthroides* (22), *Plicatolina kindlei* (21), *Missisquoia typicalis* (20), *Symphysurina minima* (16), *Hardyoides glabrus* (15), and all others (7). For ease of calculation let us say that each of the first four species is represented by 20 molt stages, *S. minima* and *P. kindlei*, three for *P. triarthoides* and *"T." gelasinata*, and none for the remaining species.

This molt-stage number we may divide into the counted number of specimens (Table 1) to obtain an estimate of the actual number of individuals represented, but before we can do this we must account for the selective introduction of convex forms. It appears that both valves of the brachiopods are convex enough to have been introduced in approximately equal numbers, and we cannot separate the original shells from the

TABLE 2.—ADJUSTED COMPOSITION OF UPPER GORGE FAUNA, EXCLUDING INARTICULATE BRACHIOPODS

Species	Number of Individuals Represented	Per Cent of Fauna
Archaeorthis crassa	39	34.2%
Glyptotrophia spinosa	26	22.8
Syntrophina carinifera	8	7.0
Dictyonema vermontense?	8	7.0
Serpulites acus	5	4.4
Geragnostus bisectus	4	3.5
Missisquoia typicalis	3	2.6
Parabolinella triarthroides	3	2.6
Symphysurina minima	3	2.6
Pseudagnostus araneavelatus	3	2.6
P. bilobus	2	1.8
"Terranovella" gelasinata	2	1.8
Hardyoides glabrus	1	0.9
Plicatolina kindlei	1	0.9
Litagnostus raymondi	1	0.9
Homagnostus sp.	1	0.9
Apheroöthis sp.	1	0.9
Orthis sp.	1	0.9
"Heteronema" sp.	1	0.9
Dirachopea sp.	1	0.9
Totals	114	100.1%

introduced ones. Therefore, since we are forced to deal with introduced brachiopods, we must also count the introduced trilobite fragments—the convex head shields.

Table 2 has been drawn up to show the estimated number of individuals represented by the collection after all corrections have been made; numbers are all rounded to the nearest full digit, and all species have been counted at least once.

The startling fact brought out by Table 2 is that this fauna, which is so obviously dominated by trilobites when specimens alone are counted (454 out of 724 actual specimens, or 63%, were trilobite remains), is actually composed of only 21% trilobites. Inclusion of the inarticulate brachiopods would apparently not seriously modify the percentages in Table 2.

POSITION OF THE *HUNGAIA MAGNIFICA* ZONE

Completion of the description of the fauna of Locality SA-NE-24 permits some additional discussion of the correlation of the enclosing strata. On the basis of available information it appears that these upper Gorge beds are most closely related to the "*Hungaia magnifica* fauna" of the "Milton dolomite" (=Clarendon Springs dolomite according to S. W. Stone, personal communication, 1950).

The *Hungaia magnifica* fauna was first found in pebbles in the Lévis conglomerate of Quebec, but it was later found in place on Cobble Hill, near Milton, Vermont.

However, the fauna at Cobble Hill has not been described or even, to my knowledge, listed except for the brachiopods described by Ulrich and Cooper (1936, 1938) and Clark (1924). Fortunately, Drs. P. E. Cloud and Franco Rasetti have examined the collections now in the U. S. National Museum and the Yale Peabody Museum, and the former has kindly furnished me with the list of identifications given below.

The fauna includes: *Aposolenopleura* cf. *A. dunbari* Raymond, 1937, (*?*) *Calymenidius tuberculatus* Rasetti, 1944, *Hungaia magnifica* (Billings), 1860, *Kainella*, *Lecanopleura?*, *Lévisella brevifrons* Rasetti, 1944, *Lévisella* sp., *Onchonotus richardsoni* (Walcott), 1913, *Onchonotus* sp., *Platycolpus* sp., *Pseudosaukia sesostris* (Billings), 1865, *Pseudosaukia* sp., *Punctularia?*, *Richardsonella* sp., and *Richardsonella?*, among the trilobites; *Finkelnburgia*, *Mesonomia* sp., *Palæostrophia elax* (Clark), 1924, *Syntrophina carinifera* Ulrich and Cooper, 1936, and *Archaeorthis crassa* Ulrich and Cooper, 1938, among the brachiopods, and the gastropod *Scaevogyra elevata* Whitfield, 1878.

Of these, *Onchonotus richardsoni* and the genera *Punctularia* and *Lecanopleura* are known in the lowest zone of the Gorge formation, but inasmuch as the last two are doubtfully identified in the Cobble Hill collection they are not strong evidence for correlation.

On the other hand, the brachiopods *Syntrophina carinifera* and *Archaeorthis crassa* seem to show a better correlation between the upper Gorge fauna and the *Hungaia magnifica* zone, and since the former has been dated as latest Trempealeauian (Shaw, 1951, pp. 99–101) the *Hungaia magnifica* zone is here stated to be the youngest Cambrian. In addition Dr. Christina Lochman has told me that a species congeneric with the trilobite "*Terranovella*" *gelasinata* is present

at the Cambro-Ordovician boundary in Montana.

SYSTEMATIC PALEONTOLOGY

BRACHIOPODA INARTICULATA
Order ATREMATA Beecher, 1891
Superfamily OBOLACEA Schuchert, 1896
Family OBOLIDAE King, 1846
Genus LINGULELLA Salter, 1866

LINGULELLA? STONEI Shaw, n. sp.

Lingulella (*Lingulepis*) *vermontensis* HOWELL, 1937 (part), Geol. Soc. America Bull., vol. 48, pp. 1155–1156, pl. 1, fig. 6 only. Remaining figures are *L. vermontensis*.

When Howell described *Lingulella vermontensis* he said that the species as then constituted might comprise more than one form, but because of the lack of sufficiently well preserved material he declined to erect more than one name. Recent collections from the Skeels Corners formation have included specimens of a new species in sufficient numbers and state of preservation to permit recognition and independent description.

In general, I do not intend to describe the inarticulate brachiopods of northwestern Vermont, for Dr. W. C. Bell has kindly consented to undertake the task, but this species is of such value in the recognition of the Skeels Corners formation that it seems necessary to name it so that it may be discussed in a forthcoming general summary of the geology of northwestern Vermont.

It is possible that this species is not a true *Lingulella* but is representative of a new genus, but no new generic name is here proposed, pending more thorough study by Dr. Bell.

The outline of both valves is oblong in front and bluntly triangular posteriorly, but a strongly developed pair of ribs radiating from the beak to the anterior angles gives the immediate impression of an acutely triangular shell. The part of the shell lying between these ridges and the lateral margins is depressed and concave; that part lying between the two ridges is flat but raised above the lateral areas. The growth lines on the central triangular area are straight and parallel to the squared anterior margin.

On the interior of both valves there is a narrow median septum; that on the ventral valve extends the full length of the shell, whereas that on the dorsal extends only half the distance to the anterior margin. The dorsal valve may also be distinguished by its rounded beak, which contrasts with the acuminate posterior of the ventral valve. The differences between *L? stonei* and *L. vermontensis* are given in Table 3.

TABLE 3.—COMPARISON OF *Lingulella? stonei* AND *L. vermontensis*

Lingulella? stonei	*Lingulella vermontensis*
1. Two heavy radial ribs present on both valves, bordering prominent triangular central area	1. Both valves evenly convex, without radial ribs
2. Growth lines straight across central triangular area	2. Growth lines curved evenly across valve
3. Specimens rarely exceed 10 mm. in length	3. Adult specimens commonly 15 to 25 mm. long

This species is common in the lower part of the Skeels Corners formation, where it is associated with an early *Cedaria* zone faunule which includes *Bovicornellum vermontensis* Howell, 1934, "*Solenopleura*" *franklinensis* Howell, 1937, *Catillicephala lata* (Raymond), 1937, *Bolaspidella schucherti* (Raymond), 1937, "*Solenopleura*" *vermontensis* Howell, 1937, *Lingulella* (*Lingulepis*) *vermontensis* Howell, 1937, and other undescribed species.

The species is named for Dr. S. W. Stone, my companion in the study of the rocks of northwestern Vermont, who collected many of the best specimens.

The figured specimen, which is chosen as the holotype, is MCZ 9346.

LINGULELLA COOPERI Shaw, new name

Lingulella vermontensis ULRICH & COOPER, 1938, not Howell, 1937, Geol. Soc. America Spec. Pap. 38, p. 51, pl. 2G, figs. 12, 13.

During compilation of a synonymic catalog of the fossils of northwestern Vermont it came to my attention that the name *Lingulella vermontensis* had been used twice; first by Howell (1937, pp. 1155–1156) for a late Middle Cambrian species, and second, by Ulrich and Cooper, as cited above, for a species from the Ordovician Providence Island limestone. Dr. Cooper has kindly suggested that I replace the homonym and it gives me pleasure to rename the species *Lingulella cooperi*.

BRACHIOPODA ARTICULATA

Suborder ORTHOIDEA Schuchert & Cooper, 1931

Superfamily ORTHACEA Walcott & Schuchert, 1908

Family ORTHIDAE Woodward, 1852

Subfamily ORTHINAE Waagen, 1884, emend. Schuchert & Cooper, 1931

Genus ORTHIS Dalman, 1828

ORTHIS sp.

Plate 18, figure 4

A single valve of what appears to be an *Orthis* has been found at SA-NE-24 in the upper Gorge formation. The specimen is not well enough preserved for specific identification.

The shape is typical of the genus, and it is mainly on this feature that the assignment is made. The ribs bifurcate a short distance from the beak.

The unique specimen is USNM 116614.

Family BILLINGSELLIDAE Walcott & Schuchert, 1908

Subfamily EOORTHINAE Walcott, 1908

Genus APHEOORTHIS Ulrich & Cooper, 1936

APHEOORTHIS? sp. indet.

Plate 18, figures 6, 7

Two specimens of what appear to be a species of *Apheoorthis* have been found in the upper Gorge formation at SA-NE-24. Both specimens are crushed and distorted. The shells have prominent, widely spaced radial ribbing crossed by a series of fine, closely-spaced growth lines. At irregular intervals there are heavier rugae parallel to the growth lines. Both of these concentric structures curve outward at the hinge line, suggesting that the valve was alate.

The specimens are USNM 116615 a, b.

Suborder SYNTROPHIOIDEA Ulrich & Cooper, 1936

Syntrophiacea SCHUCHERT & COOPER, 1931, Am. Jour. Sci., 5th ser., vol. 21, p. 247.
Syntrophiacea SCHUCHERT & COOPER, 1932, Yale Peabody Mus. Nat. History Mem., vol. 4, pt. 1, p. 154.
Syntrophioidea ULRICH & COOPER, 1936, Jour. Paleontology, vol. 10, p. 627.
Syntrophioidea ULRICH & COOPER, 1938, Geol. Soc. America Spec. Pap. 13, p. 194.

Biconvex brachiopods with unmodified delthyrium and notothyrium. Ventral valve with spondylium, prominent sulcus. Dorsal valve with short brachiophores and dorsal lamellae not enclosing muscle field; prominent fold.

Family CLARKELLIDAE Schuchert & Cooper, 1931

Clarkellidae SCHUCHERT & COOPER, 1931, Am Jour. Sci., 5th ser., vol. 21, p. 247.
Clarkellidae SCHUCHERT & COOPER, 1932, Yale Peabody Mus. Nat. History Mem., vol. 4, pt. 1, p. 155.
Clarkellidae ULRICH & COOPER, 1938, Geol. Soc. America Spec. Pap. 13, p. 211.

Smooth or ribbed Syntrophioidea commonly, but not invariably bearing a spondylium simplex. Horizontal diductor attachment plate posteriorly.

Genus SYNTROPHINA Ulrich in Weller & St. Clair, 1928

Syntrophina ULRICH in Weller & St. Clair, 1928, Missouri Bur. Mines and Geology, 2d ser., vol. 22, p. 74.
Syntrophina SCHUCHERT & COOPER, 1931, Am. Jour. Sci., 5th ser., vol. 21, p. 247. First description.
Syntrophina SCHUCHERT & COOPER, 1932, Yale Peabody Mus. Nat. History Mem., vol. 4, pt. 1, p. 155.
Syntrophina ULRICH & COOPER, 1938, Geol. Soc. America Spec. Pap. 13, p. 217.

Clarkellidae with a smooth exterior and long, closely-spaced dorsal septa.

Genotype.—Syntrophia campbelli Walcott 1908, by monotypy.

SYNTROPHINA CARINIFERA Ulrich & Cooper, 1936

Plate 18, figures 8–16

Syntrophina carinifera ULRICH & COOPER, 1936, Jour. Paleontology, vol. 10, p. 628.
Syntrophina carinifera ULRICH & COOPER, 1938,

Geol. Soc. America Spec. Pap. 13, p. 218, pl. 47F, figs. 16–22.
Syntrophina carinifera SHAW, 1951, Jour. Paleontology, vol. 25, p. 99, pl. 23, figs. 19, 20.

Diagnosis.—*S. carinifera* is distinguished from other species of the genus by having a sharply angular sulcus developed into a long "tongue" on the ventral valve, with a correspondingly high dorsal fold.

The specimens are distributed as follows: MCZ 9327–9333; in C. H. Kindle's personal collection; USNM 116616 a–i.

Family HUENELLIDAE Schuchert & Cooper, 1931

Huenellidae SCHUCHERT & COOPER, 1931, Am. Jour. Sci., 5th ser., vol. 21, p. 247.
Huenellidae SCHUCHERT & COOPER, 1932, Yale Peabody Mus. Nat. History Mem., vol. 4, pt. 1, p. 159.
Huenellidae ULRICH & COOPER, 1938, Geol. Soc. America Spec. Pap. 13, p. 194.

This family was proposed, without formal description, in 1931, for *Huenella* Walcott, 1908, and *Huenellina* Schuchert and Cooper 1931. In 1932, Schuchert and Cooper included the same genera and diagnosed the family as:

> Syntrophiacea externally like *Syntrophia* but costate or costellate. Ventral valve with pseudospondylium; dorsal brachiophore supports discrete, subparallel.

Ulrich and Cooper (1938, p. 194) changed the diagnosis, stating that the family is "characterized by a sessile spondylium"; they further subdivided the family into the Palaeostrophiinae, containing *Huenella*, *Huenellina*, *Palaeostrophia* Ulrich and Cooper, 1936, and *Plectotrophia* Ulrich and Cooper, 1936, and the Mesonomiinae, containing *Mesonomia* Ulrich and Cooper, 1936, and *Glyptotrophia* Ulrich and Cooper, 1936. This division disagrees with their own definition of the family, however, because *Huenella*, *Huenellina*, *Mesonomia*, and *Glyptotrophia* all have pseudospondylia; *Plectotrophia* appears from figures and descriptions to have a spondylium simplex, while *Palaeostrophia* has a sessile spondylium. Therefore, I suggest the following revision of the family:

Family HUENELLIDAE. Smooth or ribbed Syntrophioidea. Ventral valve with pseudospondylium in typical genera but less commonly with sessile spondylium. Dorsal septa convergent and subparallel.

Subfamily HUENELLINAE Shaw, new subfamily. Huenellidae with pseudospondylium and without cardinal process. Included genera: *Huenella* and *Huenellina*.

Subfamily PALAEOSTROPHIINAE Ulrich and Cooper, 1936. Huenellidae with sessile spondylium or spondylium simplex and without cardinal process. Included genera: *Palaeostrophia* and *Plectotrophia*.

Subfamily MESONOMIINAE Ulrich and Cooper, 1936. Huenellidae with pseudospondylium and a rudimentary cardinal process. Included genera: *Mesonomia* and *Glyptotrophia*.

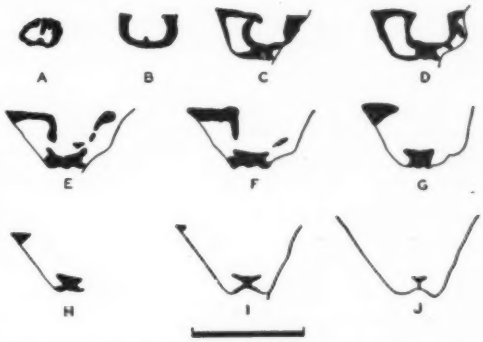

FIG. 1—Serial sections through the beak of the ventral valve of *Glytotrophia spinosa* Shaw, n. sp. Note the discrete median portion of pseudospondylium in C, D, and G. Length of bar: one centimeter.

GLYPTOTROPHIA SPINOSA Shaw, n. sp.
Plate 18, figures 22–29; text-figure 1

Exterior.—Species of typical syntrophioid shape, with prominent growth lines crossed by heavy, widely-spaced, radial costae. Many fine capillate ribs are crowded between the costae. The species is unusual among Cambrian brachiopods because it is spinose. At each growth line the heavy costae are extended outward as spines, forming an angle of about 20° with the surface of the shell in front of the spine. These structures are not the same as the spines of the Productacea, which are separate rods set into the shell. These spines are the anterior extension of the ribbing, and I propose to call them *rib-spines*. The rib-spines are long and stout (ranging up to 0.25 mm. in diameter)

and, as far as can be determined, solid. Some representative measurements, taken at random are:

Shell length	Rib-spine length
1.85 mm.	1.5+ mm.
2.2 mm.	1.4+ mm.
2.3 mm.	1.4+ mm.
2.3 mm.	2.2+ mm.
2.6 mm.	1.8+ mm.
3.4 mm.	2.1+ mm.

The tips of the rib-spines have not yet been observed.

In addition to the rib-spines, the capillate ornamentation has also developed into finer, shorter extensions at each growth-ring. These extensions are closely-spaced, needle-like structures, to which I shall apply the term "frills." The largest of these frills is less than 0.1 mm. in diameter.

Most immature ventral valves have four coarse costae and the dorsals, five to seven, but this pattern is not invariable. New costae are added by implantation between the primary set, with the first implantation commonly appearing where the shell is 2 to 2.5 mm. long, but some valves show the "second" set of costae from the smallest size. A third implantation is commonly found at the second growth ring following the second implantation.

The species is highly biconvex in the young stages, with no sign of a fold or sulcus. The fold and sulcus first appear in shells about 3 mm. long.

Ventral interior.—Serial sections (text-fig. 1) reveal a pseudospondylium sessile at the rear but free anteriorly. At three separate stages in the grinding (text-figs. 1C, D, G) a median filling (?) was discernible. The delthyrium is widely gaping and not modified by deltidial plates or xenidium (Cloud, 1942, p. 17).

Dorsal interior.—There is a low, well-defined cardinal process. Brachiophores as in *Huenella*, stout, and simple supported by low, short plates.

The holotype is USNM 116618 and figured specimens are USNM 116617a–f. Paratypes are USNM 116617g–m, MCZ 9312–9326, Univ. Wyoming IT 101–117, and in the personal collection of Dr. C. H. Kindle.

MISCELLANEOUS SPECIES

Genus DIRHACHOPEA Ulrich & Bridge in Bridge, 1931

Plate 18, figure 19

Dirhachopea ULRICH & BRIDGE in Bridge, 1931, Missouri Bur. Geology Mines, vol. 24, 2d ser., pp. 187–188.

Dirhachopea KNIGHT, 1941, Geol. Soc. America Spec. Pap. 32, p. 101.

A single, minute specimen from the upper Gorge formation at SA-NE-24 seems to belong to this genus, but because of its small size, and without other specimens no attempt has been made to name it. The specimen has a maximum diameter through the aperture of 2.3 mm. The coil is smooth, save for poorly defined growth lines. The last whorl does not seem to be free. USNM 116619.

Phylum BRYOZOA Ehrenberg, 1831

"HETERONEMA" sp.

Plate 18, figure 5; text figure 2

A single bryozoan sherd has been found in the upper Gorge formation at SA-NE-24. It is too poorly preserved to show much more than gross shape, which may be seen in the photograph and text figure.

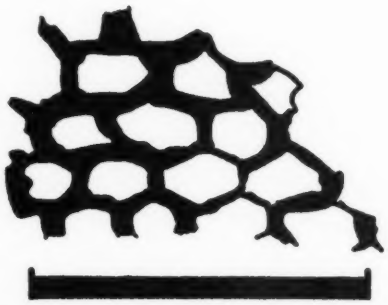

FIG. 2—Sketch of "*Heteronema*" sp. to show the arrangement of the zooecia. Bar is one millimeter long.

The arrangement of the zooecia seems to be too regular to permit certain assignment to *Heteronema*, but no other genus known to me seems to hold this form either, and I would not undertake to erect a new genus or species on such material. USNM 11620.

Phylum CNIDARIA Hatschek, 1888
Genus SERPULITES MacLeay in Murchison, 1839
SERPULITES ACUS Shaw, n. sp.
Plate 18, figures 17, 18

This species consists of small, shiny black chitinous tubes. The interior of the tubes appears to be smooth, but the outside is marked by growth lines. In their early stages the tubes are nearly cylindrical (fig. 18), but the adult portions flare quite noticeably (fig. 17).

The holotype is USNM 116621 and paratypes are USNM 116622a–c.

Class GRAPTOLITHINA Bronn, 1846, emend. Lapworth, 1875
Order DENDROIDEA Nicholson, 1872
Family DENDROGRAPTIDAE Roemer, 1897
Genus DICTYONEMA Hall, 1851
DICTYONEMA VERMONTENSE Ruedemann, 1947?
Plate 18, figures 30–31

Dictyonema schuchcrti KINDLE, 1936, not Ruedemann, 1933, Geol. Soc. America Proc. for 1935, p. 386.
Dictyonema vermontense RUEDEMANN, 1947, Geol. Soc. America Mem. 19, p. 165, pl. 3, figs.6–8.

Several fragmentary specimens found in the shaly partings at SA-NE-24 seem to show a closer affinity with this species than with the more common *D. schucherti*. All are poorly preserved, however, so the identification cannot be certain.

The figured specimens, if correctly named, extend the range of the species from the late Dresbachian Hungerford slate (the "Russell slate" of Ruedemann's memoir) to the late Trempealeauian.

The reader is referred to Ruedemann's memoir for a full description of this species as well as for figures of better-preserved specimens.

The specimens are USNM 116623.

Class TRILOBITA Knorr and Walch, 1771
Genus HARDYOIDES Kobayashi, 1938

Hardyoides KOBAYASHI, 1938, Japanese Jour. Geol. Geogr., vol. 15, nos. 3–4, p. 177.
Lévisaspis RASETTI, 1943, Jour. Paleontology, vol. 17, p. 101.
Holcacephalus (*Hardyoides*) SHAW, 1951, Jour. Paleontology, vol. 25, p. 106.
Holcacephalus (*Lévisaspis*) SHAW, 1951, loc. cit.

Rasetti noted that *Lévisaspis* was distinguishable from *Hardyoides* in the absence of a rim around the cephalon, but Dr. Christina Lochman has kindly pointed out to me that the genotype, *L. typicalis*, does bear a rim and that the original description was in error in this respect. Thus, all differences between *Hardyoides* and *Lévisaspis* seem to disappear, and the latter name is here suppressed.

With the suppression of *Lévisaspis*, the apparently gradational sequence from *Holcacephalus* Resser, 1938, to *Lévisaspis* as proposed previously and expressed by the use of subgenera also becomes inaccurate, and *Holcacephalus* and *Hardyoides* are now separated sufficiently to warrant recognition as distinct genera.

HARDYOIDES GLABRUS (Shaw), 1951
Plate 18, figures 20, 21

Holcacephalus (*Hardyoides*) *glabrus* SHAW, 1951 (part), Jour. Paleontology, vol. 25, p. 106, pl. 24, figs. 1–3 only. Figs. 4, 5 not now assigned.

The discovery of two small pygidia similar to that of "*Lévisaspis*" *typicalis* Rasetti, 1943, leads to the removal of the pygidia originally assigned to *Hardyoides glabrus* and the substitution of the new forms.

The pygidium is transverse, with nearly smooth pleural lobes, and upturned rim, and an axial lobe of five segments in addition to the articulating half-ring.

The specimens are USNM 116624a, b.

The pygidia formerly placed with this species are not reassigned and may be designated as Pygidium No. 3.

Dr. G. W. Sinclair has kindly pointed out that the name *glabrus* is not a valid Latin adjective (*glaber* should have been used), so it must be regarded only as an arbitrary combination of letters and, hence, as indeclinable.

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MANUSCRIPT RECEIVED APRIL 8, 1952.

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, PP. 147–149, 1 TEXT FIG., JANUARY, 1953

SCUTELLASTER AND *ANORTHOSCUTUM*[1]

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ABSTRACT—*Scutellaster* Cragin is shown to be identical with and to have priority over *Anorthoscutum* Lambert and Thiéry. It is be of Upper Tertiary rather than Cretaceous age.

IN 1895, F. W. Cragin described his new genus and species, *Scutellaster cretaceus* from a single poorly preserved specimen supposed to come from the "Fox Hills division" of the Cretaceous in the town of Colarado Springs Colorado. Later Reeside (1924) figured and redescribed the specimen, indicating that it was from the top of the Pierre shale rather than the Fox Hills sandstone. Whether or not this species was a clypeastrid or a scutellid echinoid, it assumed great significance because it was the earliest representative of either family. Recently Reeside (personal communication) has informed the author that searches by himself and others at the stated type locality have failed to disclose additional specimens of this echinoid. Thus it appears that there is doubt as to the origin of the type specimen.

During the preparation of the section on clypeastroid echinoids for the proposed "Treatise on Invertebrate Paleontology" it became necessary to examine *Scutellaster cretaceus* in detail. It was obvious that Reeside's (1924, fig. 2A) diagram of the basicoronal plates was inaccurate if the specimen was a clypeastroid echinoid, and furthermore if his figure was incorrect and Cragin's species was a clypeastroid, that it was an advanced member of the group, and not a primitive one as it should be because of its stated age.

Through the courtesy of Remington Kellogg, Director of the Smithsonian Institution, and the kind offices of Dr. Reeside, the holotype (now in the U. S. National Museum, no. 32702) has been made available to me for examination. Most of the upper surface of the type has been removed by grinding or some other means, so that a considerable area of the oral surface may be seen from the inside; considerable lateral crushing has occurred so that some adjacent plates are disassociated and others overlapping; and the oral surface is completely covered on the outside by a hard concretionary sandstone with a calcareous cement. Despite the above noted defects, certain features clearly indicate that this specimen is to be referred to the well-known Pacific Coast upper Pliocene species *Anorthoscutum interlineatum* (Stimpson) and that it came from the Merced formation in the vicinity of San Francisco.

The hard, dark-grey, concretionary sandstone with a calcareous cement, weathering to a rusty color, is identical to that found adhering to many specimens of *Anorthoscutum interlineatum* from the outcrops of the Merced formation along the beaches both north and south of San Francisco. The occurrence of attached spines on portions of the test is a very common occurrence on specimens of *A. interlineatum* (and very rare on other clypeastroid echinoids) and the spines on Cragin's specimen are the same kind (with a broad, relatively flat head) as found on the Merced specimens. Well-defined growth lines of the same kind are present on both the type of *S. cretaceus* and eroded or worn specimens of the Pacific Coast species; furthermore corresponding plates on the upper surface have the same shape. Finally, the visible plates on the oral surface of Cragin's type have the same characteristic arrangement (Text figure 1) as in *A. interlineatum*—an arrangement which is not found in any other echinoid genus: the two anterior interambulacral basicoronal plates are larger than the two lateral paired

[1] A contribution from the Museum of Paleontology of the University of California, Berkeley 4, California.

interambulacral basicoronal plates, and the latter two in turn are larger than the posterior unpaired interambulacral plate; in interambulacrum 5 the post-basicoronal plates are separated from the basicoronal plate by the adjacent pair of ambulacral plates; in interambulacra 1 and 4 only the posterior columns of plates are in contact with the basicoronal plates, and the first post-basicoronal plates of these two columns (1a and 4b) are considerably elongated; in interambulacra 2 and 3 both columns of post-basicoronal plates are in contact with the basicoronal plates (the normal condition in *A. interlineatum* although the specimen illustrated in Text figure 1a does not have the plate in column 3a quite touching).

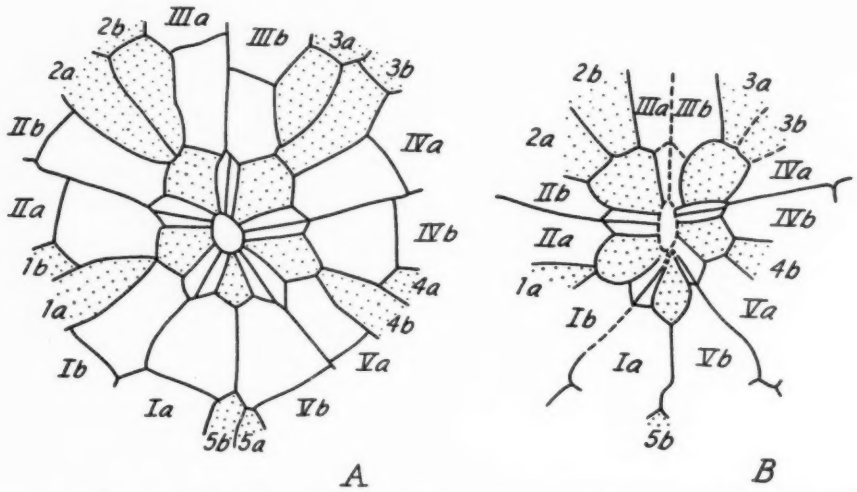

FIG. 1—*A*, *Scutella interlineata* Stimpson ×1.16. Hypotype Univ. Calif. Mus. Paleo. no. 32870, loc. A 4482, Merced formation, California. View of part of oral surface around peristome, showing characteristic plate arrangement (except for first post-basicoronal interambulacral plate in column 3a which is normally in contact with basicoronal plate). Specimen slightly deformed along antero-posterior axis so that peristome is elongated.

B, *Scutellaster cretaceus* Cragin ×0.8. Holotype, U. S. Nat. Mus. no. 32702. Internal view of plates on oral surface, reversed to compare with external view of *Scutella interlineata* in figure A. Relationships of plates considerably disturbed by lateral crushing.

The above noted features clearly indicate that Cragin's specimen is conspecific with the Pacific Coast species commonly known as *Anorthoscutum interlineatum* (Stimpson). Stimpson's specific name dates from 1856 so that it has priority over Cragin's *cretaceus*, but Cragin's genus *Scutellaster* (1895) has priority over *Anorthoscutum* Lambert and Thiéry (1914). Accordingly, the generic name *Scutellaster* should be used for those Pacific Coast species assigned to *Anorthoscutum* in Grant and Hertlein (1938, pp. 91–93), namely *Scutella interlineatum* Stimpson, *Scutella* (*Echinarachnius*) *oregonensis* W. B. Clark, *Dendraster* (*Calaster*) *oregonensis major* Kew, *Anorthoscutum oregonense quayle*i Grant and Hertlein (new name for *Dendraster* (*Calaster*) *oregonensis gibbosus* Kew), and *Dendraster* (*Calaster*) *oregonensis* Clark var. *semigibbosus* Howe. The data now available indicate that the genus *Scutellaster* (*Anorthoscutum* auctores) is restricted to the Pliocene of the Pacific Coast. As to how a specimen from the upper Pliocene of the Pacific Coast came into Cragin's possession and why it was described by him as a new Cretaceous echinoid from Colorado, we can only speculate, but similar cases are not unknown.

With *Scutellaster cretaceus* shown to be an Upper Tertiary form, there is no recorded scutellid echinoid of pre-Tertiary age and the oldest now known appears to be an undescribed species of *Eoscutella* from the middle Eocene near Martinez, California.

This latter genus is already highly specialized in some respects—particularly in having food grooves bifurcating near the peristome and in the laterally elongated test, although all the interambulacral columns are still in contact with the basicoronal plates and thus primitive in this respect. It would appear from this that there are undiscovered scutellid echinoids in pre-middle Eocene rocks. Examination of the specimen reported from the Cretaceous by Waring (1917, p. 58, pl. 9, fig. 14) as *Scutella* (?) sp. indicates that it is a spatangoid and not a scutellid echinoid and thus eliminates this record from consideration.

MANUSCRIPT RECEIVED JULY 1, 1952

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, PP. 150–152, PL. 19, JANUARY 1953

MINOJAPANELLA, A NEW GENUS OF PERMIAN FUSULINIDS

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ABSTRACT—The new fusulinid genus *Minojapanella* is described from the Lower Permian Chichibu series of the northeastern part of the Mino-mountainland of Japan with *M. elongata*, n. sp., as genotype (type species).

THE purpose of this article is to describe a new genus of Fusulinidae found in the Chichibu series of the northeastern part of the Mino-mountainland. Several years ago we collected specimens of this new genus from the limestone of Iritsu, Nishiwalamura, Hoshimaru, Waramura, and Akuda, in the vicinity of Hachiman-machi, Gujo-gun, Gifu Prefecture which are characterized by small and nearly transparent shells, with walls that are extremely thin and with septa that are strongly folded.

The specimens of this new genus from the limestone at Iritsu are associated with *Glomospira* sp., *Tetrataxis* sp., *Staffella* cf. *waageni* (Schellwien), *Schubertella* sp., *Pseudofusulina krotowi* (Schellwien), etc.; those from the limestone at Hoshimaru are associated with *Tetrataxis* sp., *Triticites* sp., and *Staffella* sp.; and those from the vicinity of Hachiman are associated with *Staffella* aff. *S. powwowensis* Thompson, *Schwagerina kagemoriensis* (Fujimoto), *Pseudofusulina crassiseptata* (Deprat), *Pseudofusulina vulgaris* var. *globosa* Deprat, etc. These associated fossils indicate that the new genus probably is of Lower Permian age.

The specimens here considered as representing a new genus closely resemble the genus *Gallowaiinella* Chen, 1937, from the Meitien limestone of China. However, the former genus is distinguished from the latter by its smaller size, more elongate form, smaller proloculus, and less dense axial fillings. Also, in the new genus the first one or two volutions are coiled irregularly to the outer volutions, and the fluting of the septa is very weak in the middle part of the shell. In *Gallowaiinella*, the coiling of the shell is compact and quite regular, the shell is planispiral throughout all of its volutions, and the septa are regularly fluted from pole to pole.

We propose the name *Minojapanella* for the genus mentioned above and are designating the only known species described below as *Minojapanella elongata*, n. sp., as the genotype (type species). Phylogenic position: we have placed *Minojapanella* in the subfamily Fusulininae. We consider that *Minojapanella* is the ancestral form of *Gallowaiinella*.

DESCRIPTION

Genus *Minojapanella* Fujimoto & Kanuma, n. gen.

Type species: *Minojapanella elongata* Fujimoto & Kanuma, n. sp.

The shell is very small and highly elongate fusiform to subcylindrical. The whorls are compactly coiled. The first one to two volutions are ovoid or subspherical and are irregularly coiled to the axis of coiling of outer volutions. The chambers of inner volutions increase in height more slowly than those of outer volutions. The number of volutions is usually five to six.

The spirotheca, which is exceedingly thin, is composed of a tectum, a diaphanotheca, and upper and lower tectoria. The tectoria are thin, discontinuous, and may be absent or thin in the outer volution. Septa are numerous and regularly and intensely fluted, except in the central part of the length of the shell. The tips of opposed folds in adjacent septa meet before reaching the floor of the chamber and divide the basal part of the meridional chambers into rhombic or hexagonal chamberlets, as shown by figure 11 on plate 19. T- or Y-shaped markings of secondary deposits are found in the chamberlets. The buccal aperture is relatively narrow. Chomata are slightly developed. Axial fillings are generally lacking. The proloculus is spherical and small, not exceeding 0.05 mm. in diameter.

TABLE 1.—MEASUREMENTS OF *MINOJAPANELLA ELONGATA* (in millimeters)

Specimen	Width of volutions							Form ratio of volutions			Thickness of spirotheca						
	0	1	2	3	4	5	6	3	4	5	0	1	2	3	4	5	6	7
38181	—	—	.097	.146	.226	.372	—	6.0	8.0	7.5	.008	.008	.008	.016	.016	.024	—	—
8350	.048	.081	.129	.178	.226	.291	.390	—	—	—	—	—	—	—	.016	.019	—	—
1083	.040	.081	.121	.162	.226	—	—	—	—	—	—	—	—	—	.016	.016	.016	.016
8311	—	.113	.146	.178	.259	.390	—	—	—	—	—	—	—	—	—	—	—	—
8313	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8317	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8310	—	—	—	.210	.275	.405	—	6.4	7.2	8.0	—	—	—	—	—	—	—	—
8311	—	.113	.146	.178	.259	.390	—	—	—	—	—	—	—	—	—	—	—	—

Specimen	Septal count					Tunnel angle (degrees)		
	1	2	3	4	5	3	4	5
8350	—	—	—	—	—	24	24	28
8311	7	13	16	22	25	20	21	28
8313	—	—	16	21	25	—	—	—
8317	—	—	17	23	30	—	27	—
8311	—	—	20	21	28	—	—	—

MINOJAPANELLA ELONGATA Fujimoto & Kanuma, n. sp.

Plate 19, figures 1–11

The shell is minute in size, highly elongate fusiform to subcylindrical in shape, slightly inflated cylindrical in its central region, and tapering gradually with slight convex slopes from center to pointed poles. The first one to two volutions are ellipsoidal and compactly coiled at a large angle to the outer volutions. The second volution has a form ratio of about 1.5, and the remaining outer volutions have form ratios of 6.4, 7.2, and 8.0, respectively. The number of whorls is usually five to six. Mature specimens of five volutions are 2.91 to 3.24 mm long and 0.29 to 0.40 mm. wide. The expansion of inner volutions is more gradual than outer ones, with heights of chambers of the first to sixth volution measuring 0.032, 0.048, 0.048, 0.048, 0.098, and 0.146 mm, respectively.

The spirotheca is very thin. Often it seems to have a single layer, but when we observe the thin slice of the same specimen turning the stage of the microscope, we find four layers composed of a tectum, a diaphanotheca, and upper and lower tectoria. The outer tectorium is not distinct and often cannot be observed. The thickness of spirotheca in the first to sixth volution measures about 0.008, 0.008, 0.008, 0.016, 0.020, and 0.020 mm., respectively.

The septa are particularly thin and slender and are extremely regularly fluted almost throughout the length of the shell. The chamberlets are rhombic or hexagonal in shape and are regularly arranged from pole to pole, giving T-, T_1-, Y-, and V-shaped markings in thin sections. These markings seem to have been made by secondary chemical action. The number of septa in successive whorls, as counted approximately, is 18, 19, 24, and 30 from the second to the fifth volution. Axial fillings are not distinct. Chomata are generally developed in the third to the fifth volution. The buccal aperture is low and narrow, being only about one-third as high as the chambers. The tunnel angle is 28° in the fifth volution. The proloculus is spherical, its wall is generally darker and slightly thicker than the spirotheca in the inner volutions, and its diameter ranges from 0.032 to 0.048 mm.

Occurrence.—The Chichibu series, Lower Permian in age, in the Mino-mountainland, Gifu Prefecture. The syntypes are in the Institute of Geology, Tokyo Gakugei Daigaku, Tokyo, Japan.

MANUSCRIPT RECEIVED MAY 15, 1952.

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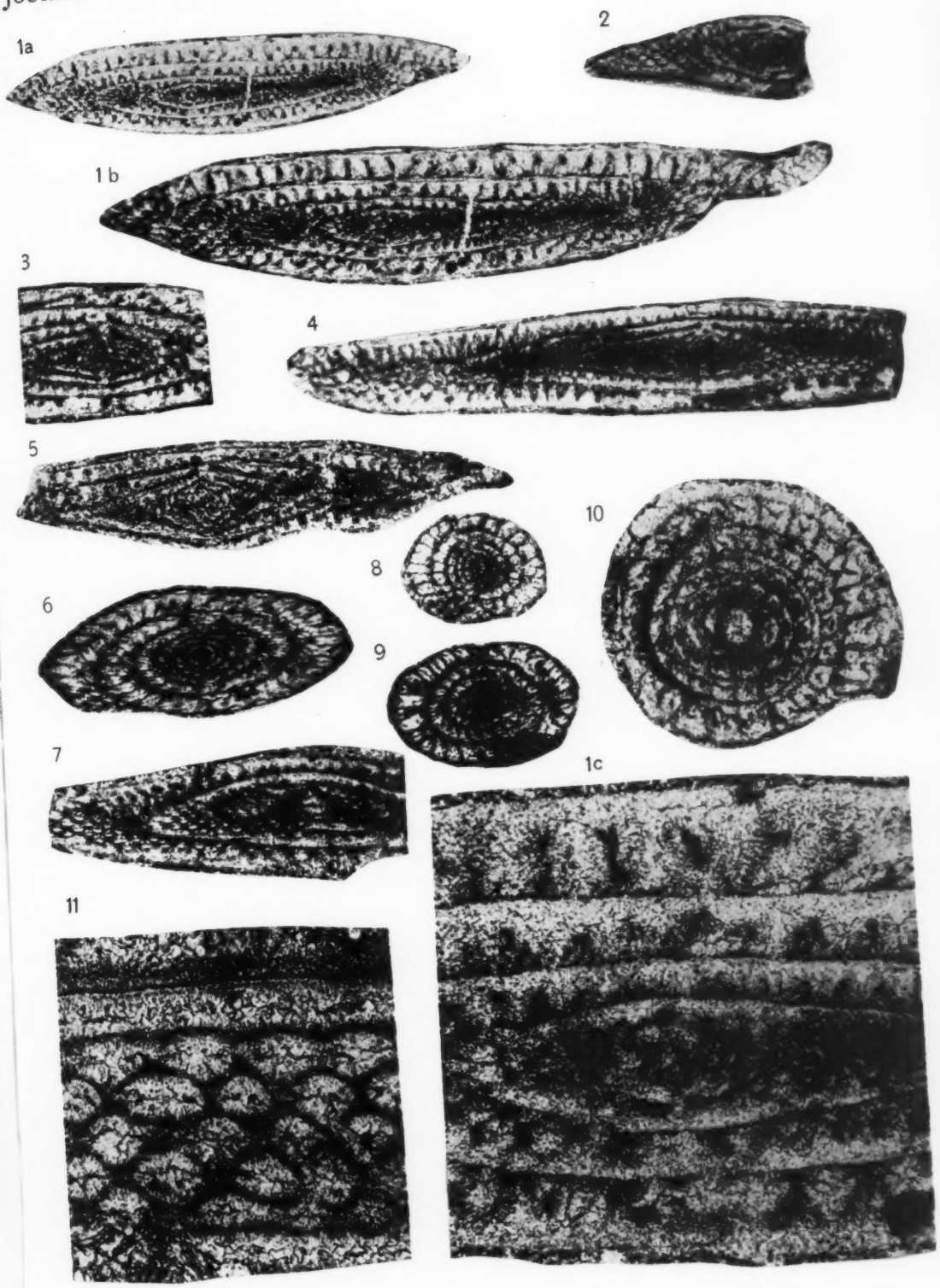
EXPLANATION OF PLATE 19

FIGS *1–11—Minojapanella elongata* Fujimoto & Kanuma, n. sp. *1a–1c*, Axial section (slightly oblique), *1a*, *1c*, showing dark layer of spirotheca, *1b*, showing transparent layer covered above and below by darker layers of spirotheca (no. 38181); *2*, axial section of a young individual (no. 1083); *3*, axial section showing chomata and tunnel (no. 1083); *4*, *5*, axial sections (nos. 8310, 1083); *6*, oblique section (no. 1083); *7*, tangential section; *8*, *9*, parallel sections (no. 8311); *10*, sagittal section (no. 1083); and *11*, tangential section showing shapes of chamberlets (no. 1083). *1a* is ×30, *1b*, *2–9* are ×45, and *1c*, *10*, *11* are ×150. All types are deposited in the Geological and Paleontological Institute of Tokyo, Bunrika Daigaku.



Fujimoto and Kanuma, fusulinid *Minojapanella*

1

2

Caster and Waering, Silurian eurypterid

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, PP. 153–156, PL. 20, 2 TEXT FIGS., JANUARY 1953

MELBOURNOPTERUS, A NEW SILURIAN EURYPTERID FROM AUSTRALIA

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AND
ERIK N. KJELLESVIG-WAERING
Helmerich and Payne, Inc., Tulsa, Oklahoma

EURYPTERIDA are known from all continents, but are best known from Northern Hemisphere materials. In contrast to the relatively great amounts of specimens from the north, Southern Hemisphere materials have so far proven very sparse, and the species comparably so. Thus the Australian discovery of material adequate for the establishment of a new eurypterid genus, herein reported, is of special interest.

McCoy's (1899, p. 13) description of *Pterygotus australis* from the Australian Silurian was the first account of Eurypterida in the Southern Hemisphere. This was based on a fragment of a body segment, possibly part of an abdominal plate, from the Upper Silurian (Melbournian) of Victoria. E. D. Gill (1951) has recorded more eurypterid fragments from possibly the same horizon in New South Wales which were determined as *Hughmilleria* sp. In our opinion, the fragment of the tergite is possibly the pretelson of a *Pterygotus*, whereas, the other fragments are insufficient for generic determination.

The only other austral eurypterids so far known are integumental scraps from Brazil and South Africa. The first of these to be encountered was mistaken (D. White, 1908, p. 589) for vegetable fragments associated with the Gondwana flora of the interglacials in the Brazilian Upper Carboniferous: *Hastimima whitei*. The following year Seward (1909) spotted the Brazilian fragments as parts of a telson, legs and tergites of a large eurypterid. Woodward (1909) concurred in this identification and Clarke and Ruedemann (1912) confirmed with documentation this change of kingdom. Recently Caster (1947) reported integument of the *Hastimima* sort abundantly present in a narrow zone of the Picos Lower Devonian in the State of Piaui, Brazil. Unfortunately none of this material warrants description. This is especially sad, for the only other record of *Hastimima* from the austral Devonian is a fragment of a body segment from the South African Witteberg series described as *Hastimima* by Seward (1909, p. 484). At that time the Witteberg terrane was considered to be Carboniferous. Kjellesvig-Waering (1948, p. 6) has questioned the assignment of the Witteberg fragment to the Brazilian Carboniferous genus. It is against such scant knowledge of the austral Eurypterida that the following Australian material is presented.

Family STYLONURIDAE Diener
Genus MELBOURNOPTERUS
Caster and Kjellesvig-Waering, n. gen.

The grouping of the compound eyes and ocelli, which are placed posteriorly on the prosoma, as well as the outline of the elongated prosoma and the type of inflated cheeks suggests reference to the Stylonuridae.

The generic traits would include: small size, bell-shaped prosoma which is emarginate in front, subrectangular compound eyes which are oblique and located, together with the interposed ocelli, in the posterior half of the prosoma.

Type species.—Melbournopterus crossotus Caster and Kjellesvig-Waering, n. sp.

EXPLANATION OF PLATE 20

FIGS. *1*, *2*—*Melbournopterus crossotus* Caster and Kjellesvig-Waering, n. sp. ×1.5; from the Silurian, Dargile Formation of Victoria, Australia. *1*, External mold of the prosoma. *2*: Impression of the interior of the prosoma.

MELBOURNOPTERUS CROSSOTUS
Caster and Kjellesvig-Waering, n. sp.
Plate 20, figures 1, 2; text-figures 1, 2

The holotype, and only known specimen, consists of a flattened dorsal shield preserved as the negative and positive of an impression of the internal part of the prosoma.

The dorsal shield is bell-shaped, broadly rounded at the posterior margin and emarginate at the anterior extremity, thus giving the shield a slightly cordate appearance. The genal angles are flaring, this being the greatest width of the prosoma, and the

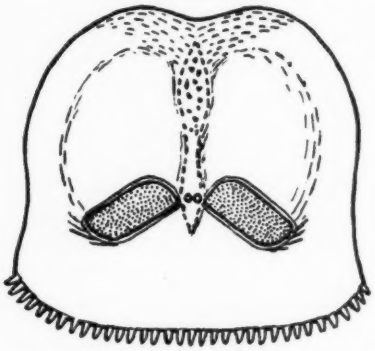

FIG. 1—Restoration of dorsal side of the prosoma of *Melbournopterus crossotus*, ×1.

antelateral angles are rounded (see pl. 20, figs. 1 and 2). The lateral margins narrow slightly opposite the compound eyes. A very narrow marginal rim surrounds the prosoma.

The dorsal shield measures 38.8 mm. in length through the center, 40.6 mm. in length through the cordate lobes, 46.6 mm. in width at the base, 42.0 mm. in width at the narrowest part, and 44.4 mm. in greatest anterior width.

The compound eyes are a distinctive and unique characteristic of the eurypterid. They are large, roughly subrectangular, and occur along with the intervening ocelli, in the anterior part of the posterior half of the dorsal shield. The eyes are obliquely situated on the shield, diverging posteriorly to an angle of approximately 120° (see text-fig. 1). In form, the elongated eyes are rounded at the inner anterior and outer posterior angles and form right angles at the outer anterior and inner posterior angles. The compound eyes are located on the dorsal shield 11.1 mm. from the posterior margin, 11.6 mm. from the genal angles, 20.6 mm. from the frontal margin and 8.5 mm. from the lateral margin. They measure 11.3 mm. in length, 5.3 mm. in width and are 3.6 mm apart. Ommatidia are not preserved. A strong fold surrounds the eye sockets on all sides; the integument is wrinkled in parallel folds at the posterior lateral corners of the eye sockets.

The ocelli occur at the posterior end of the glabella, between the lateral eyes (see text-fig. 1). Only one of the ocelli was present, and only faintly preserved. They measure less than 0.5 mm. in diameter and are located on the dorsal shield 16.2 mm. from the posterior margin, 21.4 mm. from the lateral margins and 22.2 mm. from the frontal margin.

Along the anterior, central part of the prosoma is a well-defined, raised, glabella which occurs from slightly behind the lateral eyes, between which it forms an elongate mound, then becomes evanescent at the front line of the eyes, only to expand as it becomes elevated again in the anterior part of the shield, where there is a pronounced glabellar prominence. The ocelli occur at the posterior end of the inter-orbital portion of the glabella.

Ornamentation of the shield is indistinctly preserved. Linear or slightly semilunar scales are crowded along the anterior part

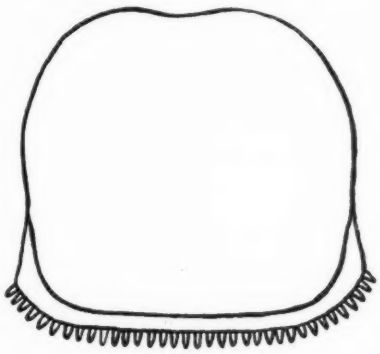

FIG. 2—Ventral side of the prosoma of *Melbournopterus crossotus*, ×1.

of the shield. This pattern of ornamentation has been previously noted on *Tarsopterella scoticum* (Woodward). The glabella is ornamented with scattered pustules. Transverse wrinkles, perhaps due to compression, occur

at the posterior lateral angles of the compound eyes. The rest of the shield appears devoid of ornamentation, except for an occasional pustule.

The posterior margin of the dorsal shield is armed with a single row of 34 evenly spaced, stout, blunt, spines. These spines are of equal length and measure 2.2 mm. in length and 8.0 mm. in width. The interspaces between the spines are subequal to the width of the spines. Each spine of the fringe appears to be separated by a sharp suture at the inner edge of the posterior doublure. The spines therefore may articulate in sockets (see text-figs. 1 and 2).

Broad, elliptical, cheek-like elevations occur in front of the lateral eyes which in many respects resemble similar structures in *Stylonurus powriei* Page, *Ctenopterus cestrotus* (Clarke), and other Stylonuridae.

The posterior doublure binds the posterior margin of the dorsal shield and comprises a narrow band of 2.6 mm. in length and extends anteriorly past the genal angles. The doublure is considerably longer at the genal angles than along the posterior margin.

Remarks.—Although the position of the eyes, general topography and surface features of the specimen seem to indicate the Stylonuridae as the proper family assignment, comparisons with known eurypterids below this level of classification are largely meaningless. The peculiar rectangular eyes and their posterior position on the prosoma are unique. The bell-shaped outline seems also without counterpart. Although the posterior border of long, flat spines is completely new, this condition might be anticipated somewhat in the elongate scales on or near the hind margin in several stylonurids and other eurypterids. The close grouping of the eyes and ocelli, the elongate prosoma, the presence of cheeks and the scale pattern suggest the Stylonuridae.

Acknowledgements.—The writers are indebted to Dr. Curt Teichert of the University of Melbourne, Australia, who furnished the material for study through the courtesy of the University of Melbourne Museum (Specimen No. 1988–89). The original discovery was made by Mr. Frank Robbins of Bendigo, Victoria, to whom all concerned are deeply grateful.

Association and ecologic suggestions.—The slabs containing the *Melbournopterus* imprints also carry many unidentifiable scraps of eurypterid integument intermixed with many monograptid stipes. The matrix is an ill-sorted argillaceous siltstone containing considerable mica and flattened mud-balls. The slabs show a fine bedding in alternate layers (approximately 0.25 in.) of cleaner siltstone and the ill-sorted siltstone. The cleaner of the silt surfaces appear to be rippled, and their under surfaces carry some "flow-marks," suggestive of the fillings by silt of the scourings eroded by gravity currents on the underlying muddy silts. This would be, then, a "Clino" environment of the Rich terminology (1951).

Locality.—The specimen came from 2.5 miles ESE. of the railway station at Heathcote, Victoria. The section has been described by Thomas (1937, pp. 64–67); it is Locality F 41/42 on the Geologic Map of the Parish of Heathcote (D. E. Thomas, 1940). This is in the midst of one of the most famous Silurian terranes of Australia.

Horizon.—Upper Silurian: from the graptolite beds (*Monograptus nilssoni* zone) in the middle part of the Dargile series. This is presumably the equivalent of the upper part of the Melbournian series (e.g., Gill, 1942; David and Browne, 1950, p. 188). The Dargile series comprises a clastic terrane of some 5000 feet in the Mt. Ida Range of the Heathcote district (idem, p. 187). According to several British and Australian writers, the graptolite fauna indicates an age equivalent to the Lower Ludlow of Great Britain. Despite the absence of critical graptolite indices in the North American deposits, this horizon is generally correlated with the Cayugan series of the New York-Appalachian region. The Dargile series carries the same graptolite association of the Jordan River series in the Walhalla synclinorium, where *Baragwanathia* and other elements of the oldest known terrestrial flora occur.

No plant material seems to have been reported from the Dargile series, however. It would be premature as yet definitely to label the life habitat of *Melbournopterus* as either marine or freshwater. The association would appear, however, to have been definitely *preserved* under marine conditions, just as was the Jordan River flora. The

overlying Dargile sandstone is richly fossiliferous with a marine fauna; the *Encrinurus* zone commences at its top.

Pterygotus australis McCoy, the only other named eurypterid from Australia, comes from the shelly marine facies of the Melbournian of the Melbourne area. The stylonurids of the Northern Hemisphere, just as in Australia, are on the other hand, usually preserved in sandstone.

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MANUSCRIPT RECEIVED APRIL 15, 1952

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, PP. 157–158, JANUARY, 1953

NOMENCLATURAL NOTES

APHELASPIS RESSER AND ITS GENOTYPE

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The generic name *Aphelaspis* Resser, 1935 (Smithsonian Misc. Coll., vol. 93, no. 5, p. 11), was established for *Conocephalites depressus* Shumard, 1861 (Amer. Jour. Sci., 2d ser., vol. 32, p. 219), as represented, in the opinion of Resser, by specimens so labeled and numbered 90172 in the collections of the United States National Museum.

The types of *Conocephalites depressus* Shumard were never figured. They are believed to have been deposited either in the collections of the Texas Geological Survey or the St. Louis Academy of Science and lost in one of the fires that many years ago destroyed the buildings that housed those institutions. Resser (1935, loc. cit., p. 12) stated, ". . . Walcott long ago set aside specimens as the species, and since they agree with Shumard's description, little doubt of their identity remains." However, a restudy of these specimens shows that they do not agree with Shumard's description, and it appears to be impossible to ascertain the identity of the specimens Shumard had available when he described *Conocephalites depressus*. It also seems probable, from my reading of Shumard's paper, that the specimens Walcott identified as *C. depressus* Shumard came from a lower stratigraphic horizon than those Shumard described.

Bridge (in Bridge and Girty, 1937, U. S. Geol. Survey Prof. Paper 186-M, p. 259, pl. 69, figs. 25, 26) illustrated the specimens used by Resser in erecting the genus *Aphelaspis*. The species *A. "depressa"* of Resser and Bridge is not the *Conocephalites depressus* of Shumard. *Aphelaspis walcotti* Resser, 1938 (Geol. Soc. America Spec. Paper 15, p. 59, pl. 13, fig. 14), is conspecific with *A. depressa* of Resser and Bridge and is the first later species to be assigned to the genus.

The concept of *Aphelaspis* as described by Resser and illustrated by Bridge is in common usage among paleontologists working with Cambrian fossils. The rejection of *Aphelaspis* (with the type *Conocephalites depressus* Shumard) as an indeterminate genus would create considerable confusion in the stratigraphic paleontology of the Upper Cambrian, where *Aphelaspis* (as used) is a common and useful zonal fossil.

I propose, therefore, to request the International Commission on Zoological Nomenclature:

1) to use its plenary powers to recognize *Aphelaspis walcotti* Resser, 1938, as the proper name for *Aphelaspis "depressa"* as used by Resser, Bridge, and subsequent authors and to designate *Aphelaspis walcotti* Resser as the type species of *Aphelaspis* Resser, 1935.
2) to place the generic name *Aphelaspis* Resser, 1935, on the Official List of Generic Names in Zoology (type species as designated above under the plenary powers, *Aphelaspis walcotti* Resser, 1938).

[1] Publication authorized by the Director, U. S. Geological Survey.

DESIGNATION OF A GENOTYPE FOR *REESIDELLA* YEN

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Recently I have described *Reesidella* to accommodate several species of Mesozoic fresh-water gastropods in "A fluviatile fauna from the Kootenai formation near Harlowton, Montana: U. S. Geol. Survey Professional Paper 233–A, Part 1, p. 6,

1951," in which I failed to mention a genotype for the genus. This unfortunate omission is rectified herein by designating *Viviparus montanaensis* Stanton (Proc. Amer. Philos. Soc., vol. 42, p. 195, pl. 4, fig. 5, 1903), as the type of *Reesidella* Yen. In addition to the genotype, the genus includes the following known species: *Amnicola golloides* Yen and Reeside, *Ampullaria? powelli* Walcott and *Reesidella? lanistoides* Yen.

A CORRECTION

CLAUDE W. HIBBARD
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It has been called to my attention by Dr. R. A. Stirton that I misquoted him in a recent publication, "Vertebrate Fossils from late Cenozoic deposits of Central Kansas," Univ. Kans. Paleo. Contrib., Vertebrata, Art. 2. On p. 4, I wrote, "On the basis of the horses, which have been examined by R. A. Stirton, University of California, the fossils from the Delmore are of the same age as vertebrates taken from Pliocene deposits near Higgins, Texas, and are either latest Clarendonian or earliest Hemphillian." The age of the horses is Hemphillian.

On page 5, Fig. 1, B, C and D, were reported as *Neohipparion* cf. *eurystyle* Cope. Fig. 1 (B) no. 6918 is *Pliohippus* (*Astrohippus*); (C) no. 6917 is *Pliohippus;* (D) no. 6915 is *Pliohippus* (*Astrohippus*).

I am most grateful to Dr. Robert Wilson, of the University of Kansas, for trying to locate the correspondence on the above teeth and for kindly sending them to Dr. Stirton for identification correction.

JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, P. 159, JANUARY 1953

REVIEWS

THREE REGIONAL CHECK LISTS OF INTEREST TO PALEONTOLOGISTS

The literature on Recent faunas, though important to the paleontologist, is not always readily accessible. Three molluscan check lists of recent years, reviewed below, may easily be overlooked because they do not appear in journals of wide circulation. All are important to anyone engaged in systematic work involving Mollusca or in stratigraphic studies that deal with Cenozoic faunules in the areas concerned.

ENSAIO DE CATALOGO DOS MOLUSCOS DO BRASIL by Frederico Lange de Morretes. Arquivos do Museo Paranaense (Curitiba, Brazil), vol. 7, art. 1, pp. 5–216, December 1949.

This is the first attempt at a molluscan check list for Brazil. It is admittedly not complete yet covers some 1,500 species of marine, land, and fresh-water forms. The arrangement is systematic, with a comprehensive alphabetical index. A bibliography of about 400 titles completes the work.

MOLLUSQUES TESTACÉS MARINS DE LA CÔTE OCCIDENTALE D'AFRIQUE by Maurice Nicklès. Manuels Ouest-Africains, vol. 2. 269 pp., 464 figs. Paris: Lechevalier (12, rue de Tournon, Paris VI^{e}), 1950. 2,800 francs.

As the type species of many widely distributed molluscan genera are from West Africa—due to the researches of the pre-Linnean naturalist Adanson—this illustrated handbook of West African marine mollusks is doubly useful. The genera are keyed out by cleverly-arranged series of tables; then each species treated by the author is briefly described and illustrated with a very satisfactory line drawing. The coverage, probably not complete, includes 459 species—292 gastropods, 160 pelecypods, 4 scaphopods. There is a bibliography of 11 titles and an unusual glossary that gives not only the derivations of the scientific names but also brief biographies of men to whom species have been dedicated. The work is indexed alphabetically by genera only.

CHECK LIST AND BIBLIOGRAPHY OF THE RECENT MARINE MOLLUSCA OF JAPAN by Tokubei Kuroda and Tadashige Habe. Tokyo: editor and publisher, Leo W. Stach, Box 121, Tokyo Central Post Office, Japan. Pp. 210+ii, 1 chart, lithoprint. April 4, 1952. $4.00.

Into 210 lithoprinted pages the authors have ingeniously packed a wealth of information about Japanese marine mollusks, covering some 4,395 species (1,048 pelecypods, 3,313 gastropods and 34 scaphopods). These are indexed systematically, alphabetically by genus, and alphabetically by species. Synonyms and nomenclatural changes of recent years are indicated, names appearing both under current and under previous assignments. Geographic range in terms of latitude and province for each valid species is given. A bibliography of about 1,700 numbered titles enables the reader to trace original references. In addition, there are some pertinent notes on distribution and on the physical characteristics of the waters surrounding Japan, with a map and bathymetric chart of the area.

The careful work of both authors and the long experience of the senior author make this a "must" for the library of anyone interested either in systematics or in Japanese mollusks. It is the key to a voluminous and scattered literature besides being a compact list of accepted names for Western Pacific shells. Several new generic and specific names are proposed.

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JOURNAL OF PALEONTOLOGY, VOL. 27, NO. 1, P. 160, JANUARY 1953

SOCIETY RECORDS AND ACTIVITIES

NOMINATIONS FOR OFFICES IN THE PALEONTOLOGICAL SOCIETY FOR 1953–54

In accordance with the provisions of Chapter III, Section 2 of the By-Laws, the Council of the Paleontological Society announces the following nominations for offices in the Society for 1953–54:

For President: HARRY S. LADD, Washington, D. C.

For Vice-President: GEORGE M. EHLERS, Ann Arbor, Mich.

For Treasurer: FRANK M. SWARTZ, State College, Pa.

For Secretary: KENNETH E. CASTER, Cincinnati, Ohio.

For Editor: WILLIAM R. EVITT, Rochester, N. Y.

Chapter III, Section 2 of the By-Laws provides that "Any twenty members may forward to the Secretary other nominations for any or all offices. All such nominations reaching the Secretary at least sixty days before the Annual Meeting shall be printed, together with the names of the nominators, as special tickets."

NOMINATIONS FOR MEMBERSHIP

In accordance with Article 3, Chapter 1, of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society. The list has been approved by Council.

CONLIN, JAMES P., Rt. 1, Burelson, Texas. A. K. Miller, M. L. Thompson.

GARNER, H. FILMORE, Geology Dept., State University of Iowa, Iowa City, Iowa. A. K. Miller, M. L. Thompson.

GLEIM, DAVID T., Geology Dept., State University of Iowa, Iowa City, Iowa. A. K. Miller, M. L. Thompson.

HEFLEY, HAROLD M., Sta. A, Box 94, Hattiesburg, Miss. R. L. Langenheim, Jr., J. W. Durham.

LIBERTY, BRUCE A., Geological Survey of Canada, Ottawa, Canada. W. A. Youngquist, A. Fischer.

MALDONADO-KOERDELL, MANUEL, Culiacán 74, Mexico 11, D.F., Mexico. A. S. Warthin, Jr., C. W. Hibbard.

MALLORY, NEIL S., Dept. of Geology, Michigan State College, East Lansing, Mich. W. A. Kelly, B. F. Howell.

MELENDEZ, BERMUDO, Francisco Navacerrada, 10, Madrid, Spain. K. E. Caster, B. F. Howell.

MURRAY, GROVER E., School of Geology, Louisiana State University, Baton Rouge 3, La. A. S. Warthin, Jr., H. V. Howe, K. E. Caster.

OAKES, MILLIS H., Dept. of Paleontology, University of California, Berkeley, Cal. J. W. Durham, R. L. Langenheim.

EATON, THEODORE H., JR., Zoology Dept., East Carolina College, Greenville, N. C. K. E. Caster, F. D. Holland, Jr.

RONAI, PETER H., 3017 Riverdale Ave., New York 63, N. Y. B. F. Ellis, P. Bronniman.

SCHELL, W. W., Box 193, Southern Methodist University, Dallas, Tex. B. F. Perkins, C. C. Albritton, Jr.

SCHULTZ, LESLIE E., 601 Sonora, Tulare, Cal. R. M. Kleinpell, J. W. Durham.

STOVER, LOUIS E., Dept. of Geology, University of Rochester, Rochester 3, N. Y. J. E. Hoffmeister, W. R. Evitt, II.

SWEET, WALTER C., Geology Dept., State University of Iowa, Iowa City, Iowa. A. K. Miller, M. L. Thompson.

TERMIER, GENEVIÈVE, Faculté des Sciences, Université de Alger, Alger, Algérie. K. E. Caster, B. F. Howell.

TERMIER, HENRI, Faculté des Sciences, Université de Alger, Alger, Algérie. K. E. Caster, B. F. Howell.

MONK, WILFRED J., 905 Iowa Street, Norman, Okla. R. D. Alexander, J. F. L. Connell, G. G. Huffman.